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Providing an ecological basis for the conservation of the Pallas's cat (Otocolobus manul)

Providing an ecological basis for the conservation of the Pallas's cat (*Otocolobus manul*)

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Abstract

Pallas's cat is a 3-5kg species endemic to Central Asia. It is Near Threatened and thought to be at risk from habitat fragmentation, a declining prey base and consumptive hunting. Moreover, it is distributed within the temperate grasslands biome, the least protected of all biomes in the world and increasingly under pressure from economic development and population growth. While the current status of Pallas's cat highlights its need for protection, its ecology has not been studied, impairing the development of conservation strategies. In this thesis I address the need for an ecological framework to support the species conservation. I conducted fieldwork for 30 months from 2005 to 2007. Pallas's cats were found to maintain large home range areas and live at very low densities. They are polygamous but appear to be non-territorial. Sex and the distribution of preferred habitats were the main factors causing variation in home range size. Pallas's cats are highly selective feeders, preferring pika over other available prey species. As pikas are 2-3 times larger than other prey species, they appear to be an optimal food item which reduces foraging costs per unit energy gain. Pika eradication programmes in China and Mongolia therefore pose a serious threat to Pallas's cats' prey base. Pallas's cat is also a habitat specialist. They largely confine activities in or near to rocky and ravine habitats. Both habitats were found to provide superior hiding and escape cover, indicating specialisation is an anti-predator strategy as used habitats had comparatively low prey availability. Marmot burrows and rock crevices were used as dens on a daily basis for most aspects of Pallas's cats' life; similar habitats were selected for denning as for foraging. Overall, the dominant influence on Pallas's cats' ecology was its susceptibility to predation. Anti-predator behaviour shaped all aspects of Pallas's cat's ecology including its habitat use, spatial behaviour, activity and where it rested, reproduced and fed. Pallas's cats apear to have several ecological traits commonly associated with extinction vulnerability, painting a bleak picture for their future conservation. Considering the diverse changes that are currently sweeping through the steppe ecosystem, significant disturbance of Pallas's cat habitat will continue to be an issue. The highest conservation priority for Pallas's cat is protection of their habitat.

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Dedication

For my son Calum

Author's declaration

I declare that the work in this dissertation was carried out in accordance with the regulations of the University of Bristol. I had help from Gantulga Jimsran and Naranbaatar Galsandorj for Pallas's cat capture and radio-telemetry. Bridget Harvey assisted in the initial stages of scat analyses. With those exceptions I declare that the work in this thesis is my own, none of which has been submitted for any other academic award. The views expressed in the thesis are those of the author.

Steven Ross

June 2009

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Abbreviations and acronyms

AIC	Akaike's Information Criterion
AIC_c	AIC corrected for small sample size
AICw	Akaike weight
ANOVA	Analysis of variance
β	Regression coefficient
°C	Degrees Celsius
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
CI	Confidence intervals
Δ	Delta
DEM	Digital elevation model
d.f.	Degrees of freedom
F	*F-ratio*
g	Grams
GIS	Geographical information system
GLM	General linear model
GPS	Geographical positioning system
h	Smoothing parameter
ha	Hectares
Hk	Cumulative diversity
IUCN	International Union for the Conservation of Nature
kg	Kilograms
kJ	Kilojoules
LSCV	Least squares cross validation
m	Metres
MANOVA	Multivariate analysis of variance
MCP	Minimum convex polygons
Mi	Mass ingested
MLE	Maximum likelihood estimation
MS	Mountain steppe
MYA	Million years ago
n	Sample size
ω	Omega (power)
p	Probability
PO	Percentage occurrence
r	Radius
Rav	Ravine
RH	Rocky hillslope
R^2	Coefficient of determination
ROC	Receiver operator curve
RSF	Resource selection function
S	Steppe
Sc	Jacobs index
SE	Standard error
UTM	Universal transverse mercator
z	Standard normal deviate

Chapter 1

Introduction

1.1. Extinction and species vulnerability

Our planet is currently entering a severe anthropogenically driven extinction event. Fossil records suggest that global extinction rates are now up to a thousand times higher than background levels (Leakey & Lewin 1995; May *et al.* 1995; Pimm *et al.* 1995). While most extinctions since the year 1600 have occurred on oceanic islands, continental extinctions are now as common as island extinctions. This is due to a change in the main causes of extinction, from introductions and overexploitation affecting island species, to present day habitat loss and degradation affecting continental biota (Smith *et al.* 1993; Mace *et al.* 2005). The unprecedented losses we have already witnessed have resulted in pressing concerns for the conservation of present-day biodiversity.

Given the current loss of biodiversity, conservation efforts must proceed with an understanding that only a small, critical fraction of the world's habitats may survive as natural or semi-natural areas (Groom *et al.* 2005). Protecting the remaining areas of viable habitat is therefore a priority. A limited amount of protection is provided by nature reserves, and further protection has been achieved in the buffer zones surrounding reserves. However, to avoid overlooking conservation opportunities, it is important that the whole landscape matrix is included in conservation planning, as a large fraction of the earth's surface is needed for the conservation of species diversity (Myers *et al.* 2000; Gaston *et al.* 2003; Groom *et al.* 2005; Ceballos *et al.* 2005). Since resources for conservation are limited, a major challenge for ecologists is to provide a solid basis to establish conservation priorities that minimise extinctions and maintain ecosystem function (Daily 1997; Margules & Pressey 2000; Ceballos & Ehrlich 2002).

To minimise extinction rates, it is important to understand a species' ecological characteristics and how they relate to extinction risk. Assessing extinction risk is

important because it permits the identification of species whose biology will predispose them to decline if threats intensify (Cardillo *et al.* 2006; Purvis 2008). Identifying the traits and mechanisms associated with a species' vulnerability ultimately provides a basis for prioritisation and the formulation of effective conservation action plans (Purvis *et al.* 2000; Schoener *et al.* 2001; Jones *et al.* 2003; Kotiaho *et al.* 2005).

Although the set of circumstances contributing to extinction risk is unique for each species, comparative studies have begun to reveal general patterns and correlates of extinction risk within groups of species. For mammals intrinsic traits associated with extinction include: large home range size, poor dispersal ability, high predation pressure, diet or habitat specialisation, low population density, small geographical range size and low reproductive potential (Purvis *et al.* 2000; Schoener *et al.* 2001; Harcourt *et al.* 2002; Johnson *et al.* 2002; Fisher *et al.* 2003; Jones *et al.* 2003; Isaac & Cowlishaw 2004; Kotiaho *et al.* 2005; Cardillo *et al.* 2006, 2008). These biological traits of organisms interplay with extrinsic factors such as human density and local environmental conditions to determine a species' likelihood of survival (Fisher *et al.* 2003; Cardillo *et al.* 2008).

1.1.1. Proactive use of knowledge

As our understanding of the factors leading to species' extinctions increases, albeit from a limited sample of species, there is increasing appreciation of the ecological information that is most important to promote species conservation. This is an important step, as it allows field projects to better focus on objective conservation goals and collect the necessary data. Data collection is still important as large gaps in our knowledge currently make assessments of species' vulnerability and ecosystem integrity difficult, hampering the development of appropriate conservation measures (Baillie *et al.* 2004). Recent studies have also found that previous 'best practice' methods, such as using biodiversity hotspots to determine conservation priorities, are overly simplistic and weak. Designing the effective protected area networks we need to conserve biodiversity is therefore likely to require a greater resolution of data on the distribution of multiple taxa and an understanding of how these species relate to ecosystems (Grenyer *et al.* 2006).

Most practical conservation decisions for reserve design and assessments are made at local and regional scales, but a suitable resolution of data is lacking for most species (Balmford & Gaston 1999; Polasky *et al.* 2000; Gaston & Rodrigues 2003; Brooks *et al.* 2004). The situation is particularly acute in remote areas of the world or hard-to-reach habitats, and for rare and cryptic species, which are logistically difficult to study, hampering the efficacy of conservation efforts. However, it is likely to make economic and performance-related sense to concentrate conservation efforts in remote areas where pre-emptive and adaptive conservation management is still feasible. The 'pre-emptive approach' concentrates on intact habitats before they become critically threatened. This has an advantage over the 'fire-fighting approach', which concentrates on highly developed areas at high risk of further habitat loss. Here, land costs are high, complex legislation exists and human interests are more likely to conflict with conservation initiatives, often resulting in escalating costs, time and complexity to conserve species (Spring *et al.* 2007). While both strategies are necessary, and public interest will always be focused on urban areas and their surroundings, there is a strong cost-benefit case to increase efforts in remote areas on little known species.

1.2. The study region

Mongolia is a large landlocked country of 1,564,116 km^2. Between Mongolia's mountain ranges, which reach upwards of 4000m, vast plateaus stretch between 1500 and 3000m (Hilbig 1995). Its high altitude and continental position largely determine the climate, which is typified by large variations in temperature (+41 to -55 $^{\circ}C$) and aridity (precipitation 25 to 600mm per annum; Gunin *et al.* 1999), with precipitation decreasing from north to south. Where precipitation drops below 300mm per year, trees cannot survive and grasses dominate the vegetation. So taiga forest dominates in the north, giving way to forest steppe to the south, then steppe, desert steppe and desert in the far south where precipitation is rare.

The Mongolian steppe is one of the last relatively undisturbed areas of the steppe ecosystem that once covered a large part of the Eurasian continent (Hilbig 1995;

Wallis de Vries *et al.* 1996; Gunin *et al.* 1999). Mongolia is inhabited by more than 2,823 species of plants (Gunin *et al.* 1999), 469 birds and 139 mammals (Clark *et al.* 2006). Mongolia's biota appears to have persisted for two main reasons: (1) Mongolia has the lowest human population density in the world, with just 1.7 people/km^2, and (2) it has a rich, and low impact, cultural heritage where half of the 2.9 million inhabitants practice traditional semi-nomadic herding, a practice that has continued for the past 14,000 years (Tumurjav 2002). Until now Mongolia has only experienced a limited amount of industrialisation and cultivation and has relatively low rates of natural resource exploitation, resulting in geographically large areas with little adverse anthropogenic impacts. The biodiversity found in Mongolia is in marked contrast to that of neighbouring regions, a warning of what could potentially become of Mongolia's biodiversity (Lhagvasuren *et al.* 1999). Currently Mongolia provides an opportunity to realise positive and significant conservation objectives, yet an increasing human population (Figure 1.1) and pressure to exploit its vast mineral wealth mean that time is running out. Conservation data are required in order to lay a foundation that promotes sustainable economic developm ent in Mongolia while maintaining its rich and unique biodiversity.

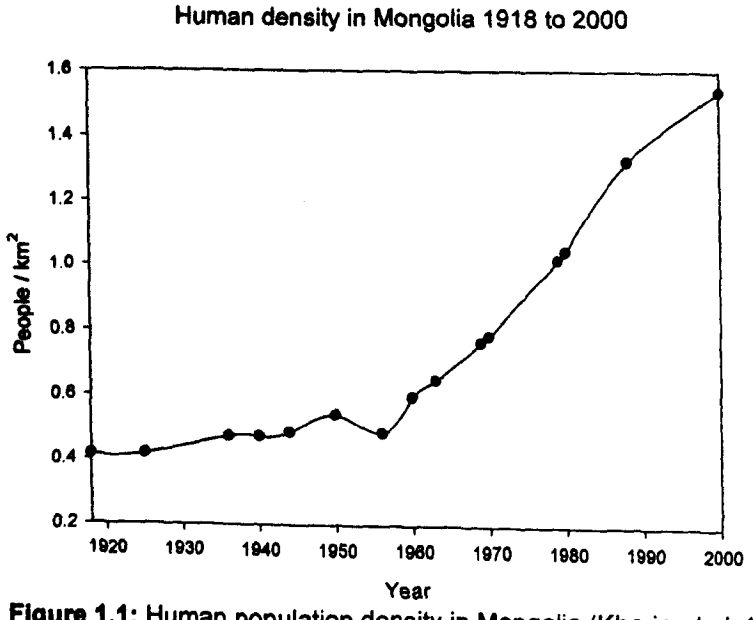

Figure 1.1: Human population density in Mongolia (Kharin *et al.* 1999; Kharin 2002).

1.3. The study species

Pallas's cat (*Otocolobus manul*) is a small (3-5kg) cat originally distributed throughout much of the Central Asian steppe (Figure 1.2). It is thought to be most abundant on the cold grasslands of Mongolia, Inner Mongolia and the Tibetan Plateau. Elsewhere it is considered vulnerable to rare and uncommon. The species is currently listed as Near Threatened in the IUCN Red List (Ross *et al.* 2008) and by CITES in Appendix 2. Pallas's cat is thought to be at risk from habitat fragmentation, a declining prey base due to vermin control programs and hunting for its fur and traditional medicines. The impact and accuracy of these pressures on Pallas's cat populations is currently impossible to assess because of the absence of ecological information on the species, and the anecdotal nature of all previous assessments.

1.3.1. Distribution and ecology

The Pallas's cat is distributed from the Caspian Sea in the west through southern Turkmenistan, Iran, Afghanistan, Baluchistan, Ladakh, western and central China, Inner Mongolia, Mongolia and Siberia (Figure 1.3; Heptner & Sludski 1992; Sunquist & Sunquist 2002; Ross *et al.* 2008). However, the paucity of records suggests that it is rare and has a very patchy distribution. Its distribution also appears to be limited by snow cover, as Pallas's cats are rarely found in areas where the mean 10-day snow cover exceeds 10cm. Most records are in mountainous areas, steppes and rocky outcrops, suggesting that these are preferred habitats (Heptner & Sludski 1992; Sunquist & Sunquist 2002).

Figure 1.2: A female Pallas's cat photographed in a mountain steppe habitat in the study area.

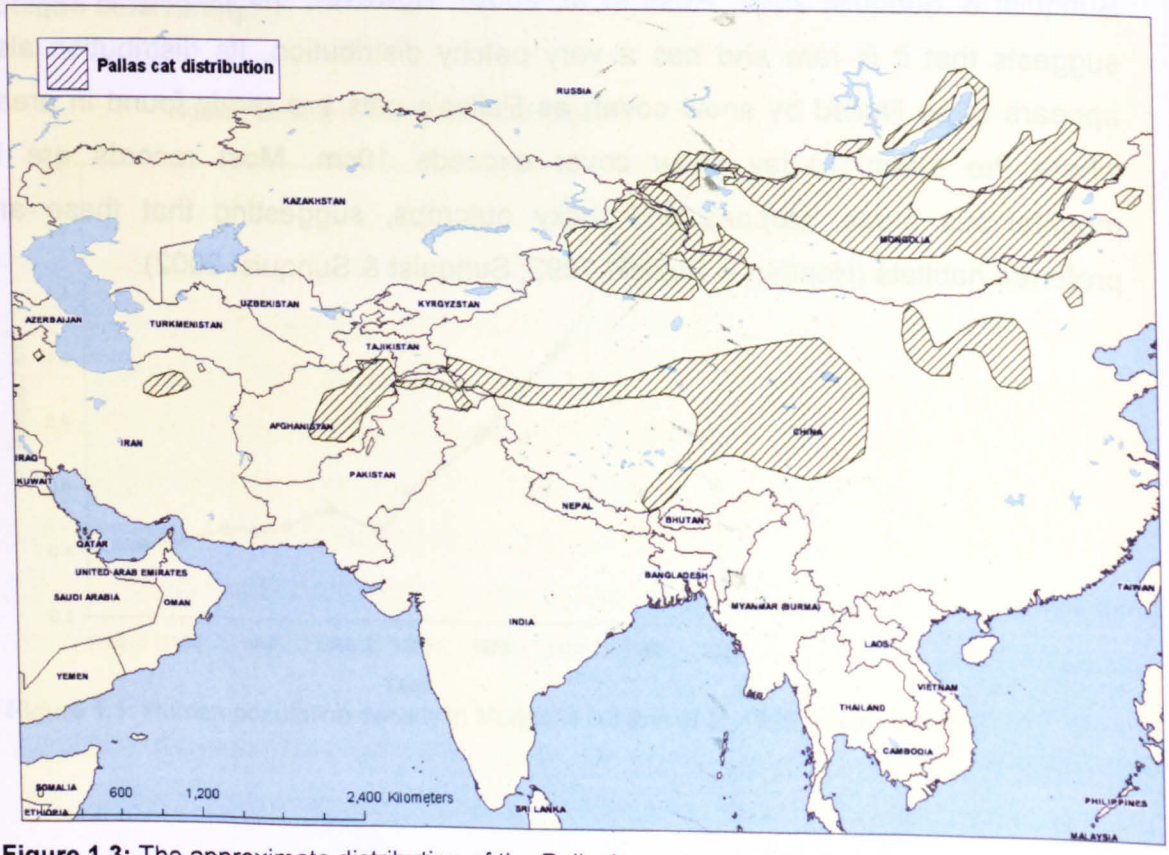

Figure 1.3: The approximate distribution of the Pallas's cat (adapted from *Ross et al.* 2008).

1.3.2. Taxonomy

Recent advances in the molecular phylogeny of the Felidae have grouped the 37 species into 8 lineages (Johnson *et al.* 2006). Morphological, biological and physiological similarities within lineages have largely confirmed the results (O'Brien & Johnson 2007). O'Brien & Johnson's (2007) analysis included the Pallas's cat in the leopard cat lineage, but with an early divergence from the other leopard cats, justifying its status as a unique genus. The leopard cat lineage split from a common felid ancestor approximately 6.2 million years ago (MYA), whereas the domestic cats split approximately 3.4 MYA. Other members of the leopard cat lineage include the Asian leopard cat (*Prionailurus bengalensis*), the fishing cat (*Prionailurus viverrina*), the flat-headed cat (*Prionailurus planiceps*) and the rusty-spotted cat (*Prionailurus rubiginosus*; O'Brien & Johnson 2007).

1.4. Aims of the study

My prime aim was to provide a comprehensive and scientifically-based platform describing the ecological characteristics of Pallas's cats and how they relate to extinction vulnerability. Based on previous studies of extinction risk, my aims were to understand: (1) whether the Pallas's cat is a specialist or generalist in terms of its diet and habitat requirements; (2) the specific habitat requirements of Pallas's cats in terms of critical denning habitat and foraging habitats; (3) the spatial ecology and density of Pallas's cats; and (4) limiting factors on the population, causing mortality or disturbance.

1.4.1. Specialisation

One of the most significant factors influencing extinction risk is specialisation (McKinney 1997; Purvis *et al.* 2000). Species avoid competition through specialisation in terms of diet, foraging strategies, or habitat selection. But specialisation also leads to an increased dependence on specific resources, resulting in lowered resilience to change (Begon *et al.* 1996). Hence, when used resources decline or become unavailable, specialists are likely to suffer more than generalists because generalists are better able to utilise alternative resources (Wilson *et al.* 1999; Harcourt *et al.* 2002; Hopkins *et al.* 2002).

1.4.2. Habitat and prey selection

The only means of demonstrating specialisation is by showing resource selection disproportionate to availability; this can be achieved by studying habitat and prey selection characteristics (Manly *et al.* 2002). Understanding resource selection is also essential in predicting the distribution of rare or threatened species, and allows for more effective conservation initiatives (Johnson *et al.* 2004). By examining which resources are necessary for a species' survival, the impact of disturbances throughout a species' range can be better understood.

1.4.3. Home range and density

The home range encompasses a species' area requirements and dispersal capabilities, both of which are important when assessing vulnerability to habitat fragmentation, edge effects and persecution (Woodroffe & Ginsberg 1998). Home range and dispersal are also important dimensions in assessing reserve design (Lamberson *et al.* 1994). Population density is critical in species assessments because low density is often associated with high extinction risk; when isolated in fragments, low density populations become smaller than those of co-occurring species with higher densities (Purvis *et al.* 2000). The spatial attributes of species vulnerability are therefore fundamental for adequate population management.

1.4.4. Limitations

Limitations refer to factors that either limit a species' use of resources due to behavioural changes, or directly reduce population size, including intra- and inter-specific competition, human disturbances and season, all of which may promote behavioural changes in resource use and limit the pool of resources available (e.g. Messier 1991). Predation has a more direct impact by top-down control of population size (Schoener *et al.* 2001). Both indirect and direct limiting factors can affect population viability, particularly when disturbances change the intensity of the limiting factors. For example, predators may increase their relative abundance in response to habitat disturbances or due to an association with humans (e.g. domestic dogs). Limitations are therefore the natural or anthropogenic controls, which directly or indirectly influence population size.

1.5. The study area

The study was located in the Hustain Nuruu National Park buffer zone, 47° 47'N, 106° 01'E, Central Mongolia, Altanbulag County, 100 km south-west of Ulanbaatar (Figure 1.4). The climate was typically continental; during the 3-year study mean annual temperature was -1.2°C, with highs of 38°C and lows of -43°C. Annual precipitation was 165mm, with over 80% falling in summer (Figure 1.5). Low winter precipitation combined with strong winds and grazing by domestic livestock often left the soil bare by spring, leading to frequent dust storms during spring and early summer.

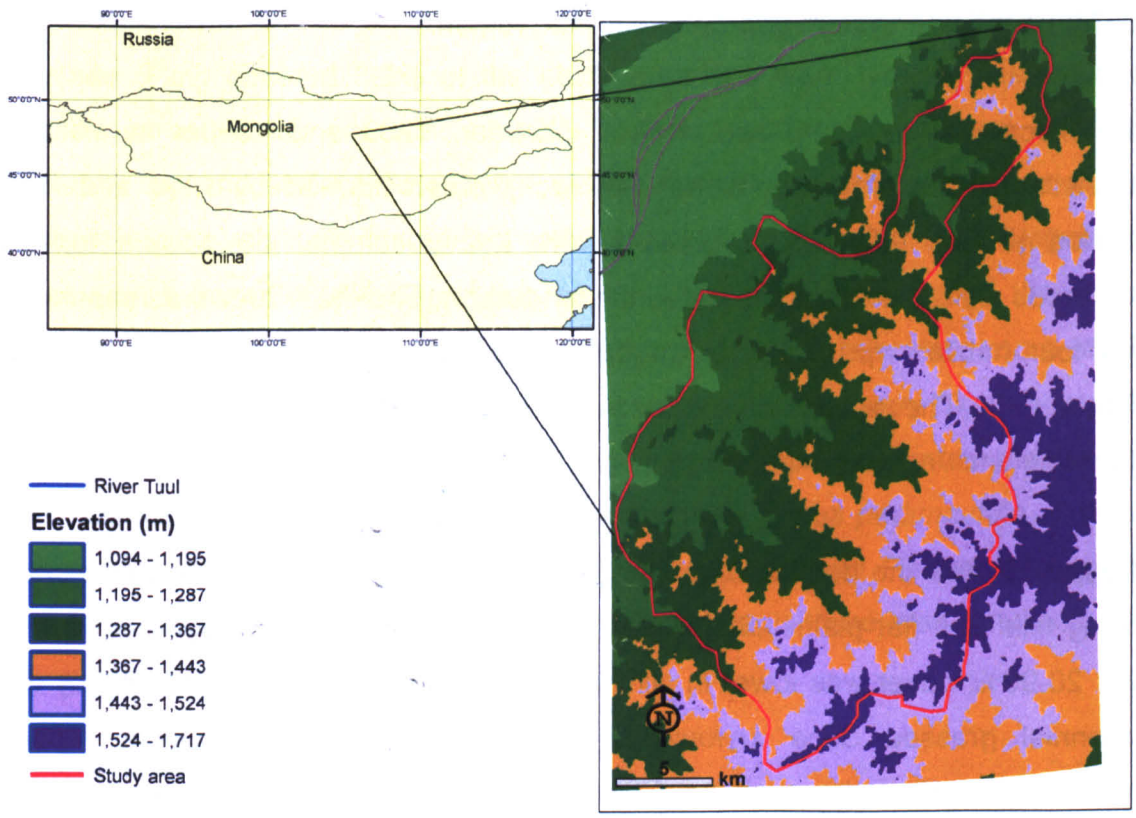

Figure 1.4: The study area's topography and position in Mongolia, projection - WGS 1984 UTM Zone 48.

1.5.1. Habitat classification

All habitats in the study area were mapped by riding habitat boundaries on an off-road motorcycle with a Garmin GPS (Garmin, Hampshire, UK) fixed to the handlebars. For ravines the centre of each ravine was tracked and then a 15m boundary added on either side in a GIS database. The GPS tracklogs were downloaded and the series of points joined and mapped into habitat polygons

within ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, California, USA). The mapping error caused by GPS accuracy was approximately 10-15m. The summer and winter camps of local nomadic herdsmen were also mapped using a hand-held GPS. A digitised 1:100,000 topographical map of the study area was converted into a digital elevation model (DEM) using linear interpolation within ArcGIS 9.2 (ESRI, Redlands, California, USA); the resolution of the DEM was set at 20m. The DEM was exported into ArcGIS 9.2 and a spatial adjustment carried out using the GPS coordinates of 45 mountain peaks as ground-truthing points. The DEM was fixed into a Universal Transverse Mercator (UTM) coordinate system appropriate for the region.

The mapped area comprised 418km^2 between 1200 and 1680m in altitude, consisting of rounded mountains with rocky crests formed by wind and frost erosion (Figure 1.5). Water erosion from heavy summer downpours formed numerous dry ravines that dissected the landscape. The study area was separated into four habitat types: steppe, mountain steppe, rocky hill-slope and ravines (Figure 1.5). The habitat categories were based on differences in topography, substrate and vegetative cover and physiognomy.

Steppe (S) was the dominant habitat (70.4% of the study area) and consisted of rolling hills and flat plains. Slope was generally less than 10°. Vegetation cover was 20-90%; cover was lower in winter than summer and was dominated by the perennial grasses *Stipa krylovii*, *Leymus chinensis* and *Agropyron repens* interspersed with forbs such as *Chenopodium album*, *Allium amphibolum* and several *Artemisia* species. Shrubs were rare, since steppe was grazed intensively by livestock.

Mountain steppe (MS) covered 19.9% of the study area and was mountainous with slopes >10°. Vegetation cover varied from 50-90% and was dominated by grasses such as *Festuca lenensi*, *Stipa krylovii* and *Agropyron cristatum* interspersed with small amounts of shrub cover, including *Spiraea aquilegifolia*, *Caragana microphylla* and sage (*Phlomis tuberosa*). Upper slopes had higher

plant diversity, including *Festuca sibirica*, *Galium verum*, *Serratula centauroides* and *Schizonepeta multifida*. Mountain steppe was grazed intensively by livestock.

Rocky hillslope (RH) covered 6.6% of the study area and had diverse vegetation but low vegetative cover of 20-60%. Representative species included dwarf shrubs dominated by *Caragana microphylla*, with *C. pygmaea* and *Caryopteris mongholica*. Grasses such as *Festuca lenensis*, *F. sibirica* and *Stipa krylovii,* and forbs such as *Thymus vulgaris*, *Schizonepeta multifida*, *Erysimum flava*, *Galium verum* and *Thalictrum petaloideum,* were abundant.

Ravines (Rav) covered 3.2% of the study area and were typically steep-sided, with a coarse, sandy soil which rapidly absorbed water. The stream bed was generally dry and surface flows were always flash floods, although groundwater flow provided a relatively favourable water supply for vegetation. Total vegetation cover varied from 20-90% depending on the habitat that surrounded the ravine and the disturbance regime. Ravines in flatter steppe habitats were more stable and had better soil structure, which was associated with a very high vegetation cover and a higher density of shrubs than ravines in sloping mountain steppe and rocky hillslopes. Characteristic species included *Amygdalus pedunculata*, *Spiraea aquilegifolia*, *Caragana microphylla*, *Agropyron repens and Rheum undulatum*, with occasional Siberian elm (*Ulmus pumila*), although there was only one fully grown elm in the study area.

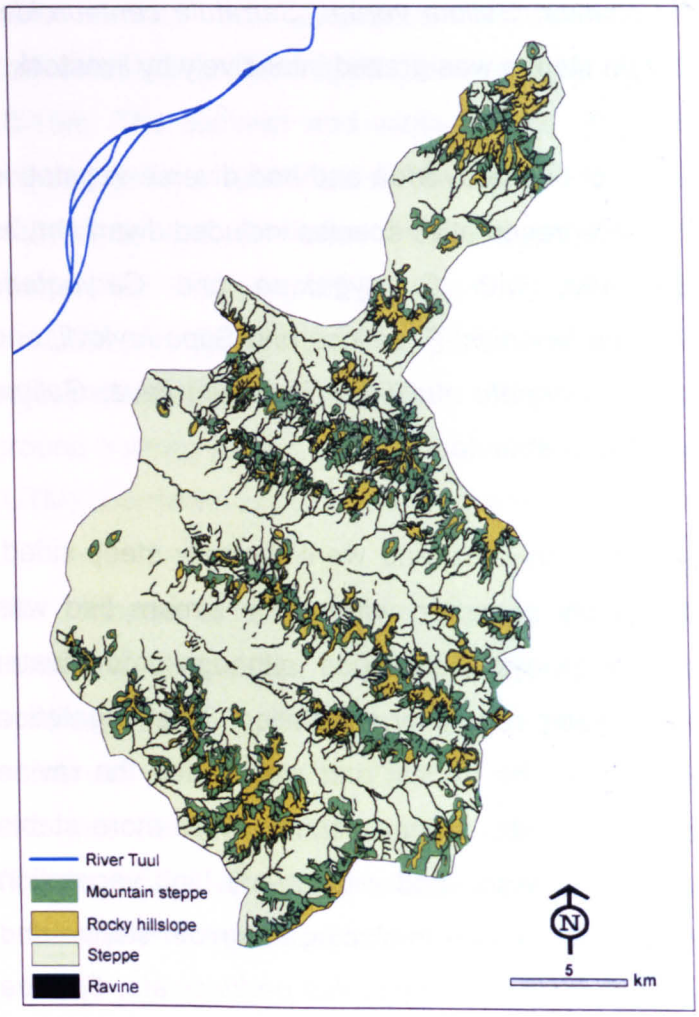

Figure 1.5: Habitats represented within the study area, mapped using a GPS attached to the handlebars of an off-road motorcycle, projection - WGS 1984 UTM Zone 48.

1.5.2. Seasons

Seasons in the study area were best defined by temperature. Once the average temperature fell below zero, vegetation froze and ceased to grow, small mammals reduced their activity and hibernating animals (jerboas, hedgehogs and marmots) retreated to hibernacula. So I divided the year into two parts, summer - April 15th to October 14th, when average daily temperature was above 0°C, and winter - October 15th to April 14th, when average daily temperature was below 0°C (Figure 1.5).

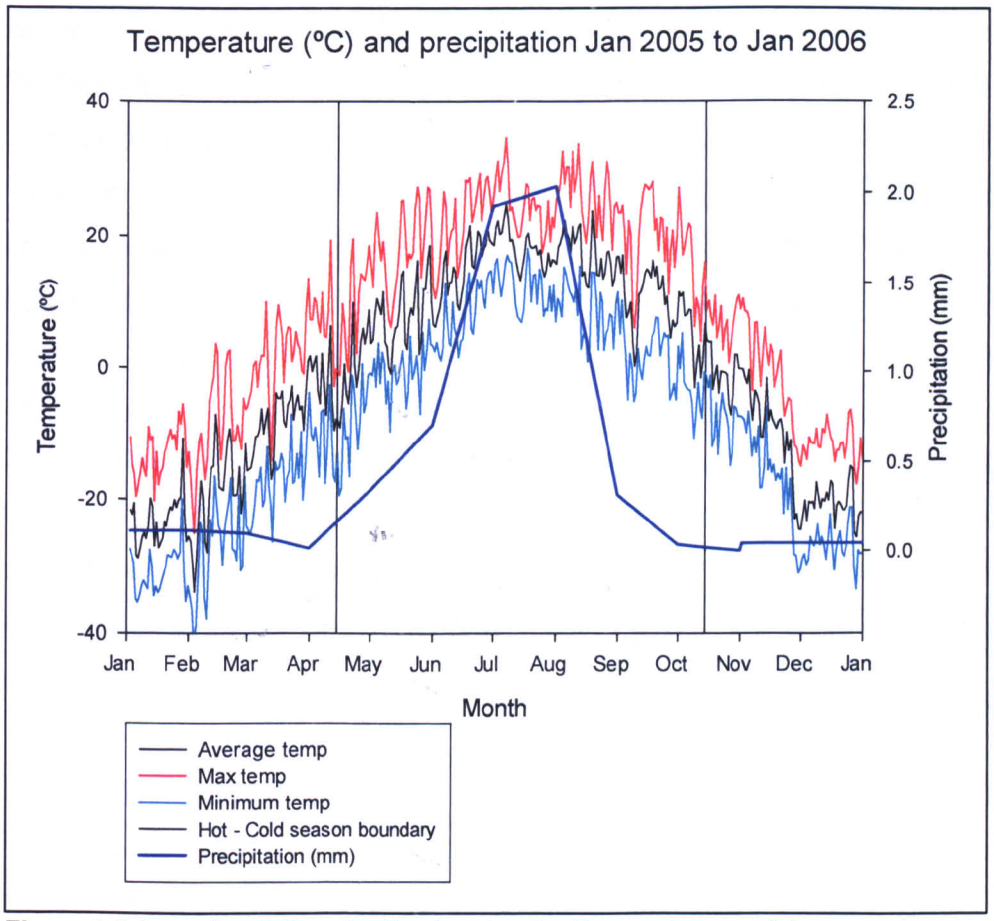

Figure 1.6 Annual variations in climate, showing the maximum, minimum and mean daily temperature and precipitation (data from Altanbulag weather station, Töv).

1.5.3. Wildlife of the study area

The study area contained a diverse assemblage of mammals. Large ungulates included Mongolian gazelles (*Procapra gutturosa*), red deer (*Cervus elaphus*) and Argali sheep (*Ovis ammon*). Small mammals included the long tailed souslik (*Spermophilus undulatus*), Mongolian gerbil (*Meriones unguiculatus*), mountain voles (*Alticola semicanus*), Daurian pika (*Ochotona daurica*), Russian dwarf hamster (*Phodopus campbelli*), Chinese striped hamster (*Cricetulus barabensis*), Brandt's vole (*Lasiopodomys brandtii*), Siberian jerboa (*Allactaga sibirica*), together with the larger Siberian marmot (*Marmota sibirica*), tolai hares (*Lepus tolai*) and Daurian hedgehogs (*Mesechinus dauuricus).* A detailed description of small mammals as potential prey species is given in Table 1.1. Predators sympatric with Pallas's cats in the study area included gray wolf (*Canis lupus*), corsac fox (*Vulpes corsac*), red fox (*V. vulpes*), Eurasian lynx (*Lynx lynx*), Siberian

polecat *Mustela eversmanni*, Marbled polecat (*Vormela peregusna*) and Eurasian badger (*Meles meles*). Large birds of prey included cinereous vultures *(Aegupius monochus)*, golden eagle *(Aquila chrysaetos)*, steppe eagle (*A. nipalensis*), upland buzzard (*Buteo rufinus*), rough legged buzzard (*B. rufinus*), eagle owl (*Bubo bubo*) and saker falcon *(Falco cherrug)* among many others. During spring and autumn, the wetland of the Tuul River is an important foraging stop for migratory birds, many of which are in transit to and from Lake Baikal 400km to the north. The most common group of insects were grasshoppers (Orthoptera), and cicadas (Hemiptera) which can become extremely common in dry and hot summers. Beetles (*Coleoptera*) were also present.

Table 1.1: Small prey species found in the study area, the survey method used to assess their abundance and their general behaviour: (1) observed during this study, (2) Walker (1975), (3) Wund & Myers (2006), (4) Zhang *et al.* (2003), (5) Wang *et al.* (2003), (6) Chapman & Flux (1990).

Species	Survey	Description
Mongolian gerbil (*Merinomes ungulatus*)	Trapped	**Activity**: crepuscular, diurnal[1] **Food:** Green shoots, roots, seeds, bulbs[2] **Wintering behaviour:** stores food, reduced activity[1]
Mountain vole (*Alticola semicanus*)	Trapped	**Activity**: diurnal, nocturnal[1,2] **Food**: stems and leaves of herbaceous plants[2], bark of woody shrubs[1] **Wintering behaviour:** stores food, reduced activity[1,2]
Striped dwarf hamster (*Cricetulus barabensis*)	Trapped	**Activity:** crepuscular, nocturnal[1,2] **Food:** Green shoots, roots, plant seeds and invertebrates[2,5] **Wintering behaviour:** reduced activity[1], entering torpor[3]
Russian dwarf hamster (*Phodopus campbelli*)	Trapped	**Activity:** nocturnal [3], occasionally active during the day[1] **Food:** Green shoots, roots, seeds, bulbs[3] **Wintering Behaviour:** reduced activity[1], entering torpor[3]
Brandt's vole (*Lasiopodomys brandtii*)	Trapped	**Activity:** diurnal, crepuscular[1] **Food:** leaves, stems and roots of grass and herbs[5], known for its food dependent eruptive dynamics[4] **Wintering behaviour:** reduced activity[1], stores food in burrow
Long-tailed souslik (*Spermophilus undulatus*)	Trapped	**Activity:** crepuscular, diurnal[1] **Food:** seeds and green parts of plants and insects **Wintering behaviour:** hibernates[1]
Daurian pika (*Ochotona daurica*)	Sign surveys	**Activity:** diurnal, crepuscular[1] **Food:** grasses, herbaceous plants[6] **Wintering behaviour**: active, stores food in burrow[1]
Siberian jerboa (*Allactaga sibirica*)	Distance spotlight surveys	**Activity:** nocturnal[1] **Food:** seeds, insects and the succulent parts of plants[3] **Wintering behaviour:** hibernates[1]
Tolai hare (*Lepus tolai*)	Distance spotlight surveys	**Activity:** nocturnal[1] **Food:** leaves and stems of plants, bark **Wintering behaviour:** active[1]
Daurian hedgehog (*Mesechinus dauuricus*)	Distance spotlight surveys	**Activity:** nocturnal[1] **Food:** insects **Wintering behaviour:** hibernates[1]

1.6. Thesis structure

In **Chapter 2** I consider the spatial ecology and factors that influence home range size of Pallas's cats. I first investigate the home range size of male and female Pallas's cats and test for seasonal differences. I use home range overlap and the dynamic interactions between cats to understand the social system of Pallas's cats. Finally, I test the influence of landscape configuration within and surrounding home ranges as factors affecting home range size variation using multiple regression.

In **Chapter 3** I investigate the feeding ecology of Pallas's cats. I reconstructed their diet using faecal analyses, and explored differences in diet and niche breadth on a seasonal and sexual basis. Prey density was measured using trapping and sign surveys, allowing prey selection to be measured against prey availability using compositional analyses.

In **Chapter 4** I investigate the foraging habitat selection of Pallas's cats using resource selection functions and a used – available design. Habitat selection is separated by sex and season. Data describing cat mortality, seasonal condition of Pallas's' cats, prey biomass and the cover provided by the available habitats are used to explain habitat selection patterns.

In **Chapter 5** I continue to examine habitat selection by considering the factors associated with critical denning habitats for Pallas's cats. Selection is tested for habitats and resources surrounding dens at different distances, rather than the structural attributes of the den itself. Again I use a resource selection function framework to describe the selection of den habitat using a used – available design.

In **Chapter 6** I consider the data from the previous chapters alongside data on density, dispersal, reproduction and survival to provide a preliminary vulnerability profile of Pallas's cats.

Chapter 2

The spatial ecology of Pallas's cat and determinants of home range size

Summary

1. Spatial ecology is an important aspect of species conservation as it incorporates social structure, spatial needs and the potential risks an animal may encounter.
2. I used radio-telemetry to collect spatial data on 29 Pallas's cats.
3. I calculated home ranges on seasonal and annual bases for males and females to test seasonal and sexual differences in home range size, and measured the static and dynamic social interactions between individuals.
4. I quantified habitat configuration within concentric circles with radii of 500, 1000, 2000 and 3000m from the home range centre and modelled the influence of habitat configuration on home range size.
5. Pallas's cats had unusually large home ranges that varied substantially between individuals. Males had significantly larger home ranges than females but season did not have a significant effect on home range size. My data indicated that Pallas's cats are polygamous but non-territorial.
6. Female Pallas's cat home range size was reliably predicted by the quantity and orientation of preferred habitats; space use was found to be a function of the distribution of critical habitat resources.

2.1. Introduction

Ecologists have long sought to identify the environmental and ecological traits that influence a species' use of space (Gittleman & Harvey 1982; Sandell 1989; Tufto *et al.* 1996; Börger *et al.* 2008). Quantifying the factors responsible for home range use facilitate predictions about how animals will respond to changes in their environment and provide insights into their relative sensitivities to disturbance. For

example, the home ranges of focal species must be considered when designing or assessing the effectiveness of protected areas (Caro 1998). Home range size is also important when making assessments of the vulnerability of a species to habitat fragmentation, edge effects and persecution (Woodroffe & Ginsberg 1998).

Spatial patterns are thought to be associated with the distribution of limiting resources and are functions of the species' social system and an individual's sex (Schoener 1981; Pierce *et al.* 2000; Mitchell & Powell 2004). Carnivores may also adjust home range size with prey availability, since they may have to travel more widely to obtain sufficient resources when food is scarce (Litvaitis *et al.* 1986; Powell *et al.* 1997; Herfindal *et al.* 2005). However, home ranges are not simple extensions of carnivore bioenergetic requirements, and the relative influence of prey availability is likely to change with prey ecology and the energetic requirements of the predator. Prey is therefore expected to be a more dominant factor in the lives of large carnivores with large energy budgets that hunt clumped and mobile prey, than for small carnivores with more modest energy needs and more evenly dispersed prey resources (Carbone *et al.* 2007). Small carnivore spatial patterns may also be influenced by the risk of interspecific predation (Donadio & Buskirk 2006), since they need to make habitat-based trade-offs between food and safety (Lima & Dill 1990; Brown & Kotler 2004). The home range areas of small carnivores should therefore be more dependent on the configuration and properties of surrounding habitats than their larger counterparts. However, while the effects of habitat configuration on space use has been demonstrated for herbivores (Kie *et al.* 2002; Anderson *et al.* 2005; Said & Servanty 2005), similar studies on the influence of habitat configuration on space use by carnivores are lacking. This is despite the factors affecting space use being key to effective conservation because they describe the underlying stimuli influencing species' spatial patterns, thus connecting animals to their ecosystems.

Despite habitat degradation being cited as one reason for the decline of Pallas's cat, there is no information on their spatial organisation or requirements. Therefore I used radio-telemetry data to understand five main aspects of Pallas's cat spatial ecology: (i) Pallas's cat' home range size; (ii) sexual influences on home range size; (iii) the influence of sociality on spatial patterns; (iv) the influence of seasonal

prey availability on home range size; and (v) the effect of habitat configuration on home range size. As the study area had a highly seasonal climate, and prey abundance varied dramatically between seasons, I expected Pallas's cats to increase their home range size to compensate for decreased prey availability in winter, corresponding with general predictions for carnivores (Harestad & Bunnel 1979). However, as Pallas's cats are subject to interference competition and available habitats provided different levels of predator cover, I also predicted that habitat configuration would affect home range size.

2.2. Methods

2.2.1. Pallas's cat capture

Several methods were used to locate and capture Pallas's cats. They are a cryptic species, and locating them was critical to the success of the study. In all, 29 Pallas's cats (13 males and 16 females) were captured between January 2005 and October 2007 using five main techniques: (1) cats were spotted from the tops of hills by scanning the surrounding area with binoculars. This was done both deliberately and opportunistically when radio-tracking (Hilltop method); (2) moving Pallas's cats were spotted opportunistically while travelling cross-country on a motorcycle or jeep (Encounter method); (3) local people spotted Pallas's cats while herding their livestock and chased them into a burrow; captures were then reported immediately to me or my field assistants (Local person method); (4) spotlighting was used to locate Pallas's cats while out on routine spotlighting surveys (Spotlight method); (5) leg-hold traps (Victor, softcatch # 2 & 3, Euclid, OH, USA) were used in combination with commercially available and self-made lures to attract Pallas's cats to enter the trap (Leg-hold method). The hilltop method produced most captures but was the most labour intensive and most frequently used method. Leg-hold trapping was used the least frequently as it was only initiated in the final year of the study, but had a relatively high success rate (Table 2.1).

Table 2.1: Percentage of captures by each method (n = 29 captures).

Method	Hilltop	Encounter	Local person	Spotlight	Leg-hold
%	38%	28%	21%	7%	7%
n	11	8	6	2	2

On sighting a cat it was chased until either it could be tripped-up or it stopped and remained motionless (a Pallas's cat anti-predator strategy); it was then caught by hand. Alternatively, cats often sought refuge in an underground burrow, from which they were dug out. Thirteen cats (48%), captured after sighting, were captured by hand and 14 (52%) were dug out. Once caught, the cat was restrained and put into a hemp capture bag to reduce stress, weighed with a Pesola spring scale (Pesola AG, Baar, Switzerland) to the nearest 125g. The cat was then restrained without anaesthesia, a VHF radio-collar attached, aged by inspecting teeth wear and a general health assessment made for scars, injuries, hair loss and ectoparasites. The cat was then released at the point of capture and observed until it took cover. It was monitored closely over the next 48-hours using radio-tracking. No injuries were inflicted on any Pallas's cats using the capture methods, and post-capture behaviour was always normal and without any unusual movement responses away from the capture site. Animal trapping and handling techniques met the guidelines suggested by the American Society of Mammalogists (Gannon *et al.* 2007) and procedures were approved by the University of Bristol Animal Services Unit, UIN Investigation Number (UB/05/010).

2.2.2. Radio-collaring and radio-tracking

I used VHF radio-collars (M1830, Advanced Telemetry Systems, Isanti, Mn, USA) in the 164-MHz frequency range. The pulse rate was 40ppm, which increased to 80ppm when stationary for more than 12hrs; this was used to detect mortality. Battery life was a minimum of 421 days. The collars had a protruding whip antenna and weighed 40g each i.e. 0.8 to 1.3% of body mass. Signals were received using a Communications Specialists R1000 receiver (Communication Specialists Inc., Orange, CA, USA) and a handheld 3-element Yagi antenna (AF Antronics, Inc. Urbana, IL, USA).

The radio-collar's signal was mostly heard as an arc rather than a point; I took the bearing at the midpoint of this arc, either by recording the direction of the loudest signal or by recording the signal null on either side of the arc and calculating the midpoint (Springer 1979). Telemetry bearings were taken after taking 1-3 positional bearings, which served to locate the Pallas's cat and move closer, thus reducing telemetry error by minimising the distance between the cat and the observer. Once close to the Pallas's cat (100 to 1000m) a minimum of 3 bearings were used to estimate cat's location (63.6%) or it was approached until sighted and a direct GPS location taken (36.4%). Radio-collared Pallas's cats were located on average every 3 days (range 1-5 days). Radio-tracking was mostly carried out during early morning and the evening, coinciding with activity peaks (Appendix 1). The majority of locations were classed as active (86%), based on signals with erratic strength and pitch (Nams 1989).

2.2.3. Radio-location error

I used the maximum likelihood estimation (MLE; Lenth 1981) to estimate locations from triangulation data within Locate III software (Nams 2006). Triangulation accuracy and precision were estimated using the location error method (LEM) which measures the distribution of distances between estimated and known locations of radio-transmitters (Zimmerman & Powell 1995). Two methods were used to obtain known collar locations: (1) radio-collars were placed in all available habitats in the study area (n=19) and (2) after estimating a cat's position using triangulation and noting they were inside a den, the den's real position was recorded and taken as the known location (n=11). The mean areal error (95% confidence circle) for telemetry locations was calculated using the formula:

Error Area (Ea) = πr^2

where: radius (r) is the standard deviation of errors multiplied by 1.96 (z statistic) (Zimmerman & Powell 1995).

2.2.4. Home range estimation

To establish whether home ranges existed, I tested whether individuals exhibited a site fidelity pattern in their movement paths. I used the 'site fidelity test', which is

an extension of the Monte Carlo random walk test (Spencer *et al.* 1990), within the Animal Movement Analyses Extension for ArcView 3.3 (Hooge & Eichenlaub 2000). One hundred simulations were run for each cat, starting at the first fix taken during the respective season and using a step length equal to actual step length, and a randomly generated turning angle. For each walk the mean squared distance from the centre of activity (arithmetic mean) and the linearity of the path were measured, which were measures of data dispersion (R^2) and of directed movement or linearity (L), respectively. The actual movement path' values were then compared with the ranked values of the random walks to determine significance. To be site-faithful, the animal's real locations should exhibit neither significant dispersion (R^2) nor significant linearity (L) (when 95% of random movement paths have higher R^2 and L values) (Hooge & Eichenlaub 2000). Fidelity was subsequently shown for all non dispersing cats.

Home ranges were estimated using kernel utilisation distributions and minimum convex polygons (MCPs), to provide the most accurate measures of home range and provide comparative measures with previous studies (Worton 1989; Harris *et al.* 1990). Least squares cross validation (LSCV) was used to estimate the smoothing parameter (h) for fixed kernel estimates, as this is the most favoured method to define home range boundaries (Seaman & Powell 1996). Home ranges were calculated in the Animal Movement Analyses Extension for ArcView 3.3 (Hooge & Eichenlaub 2000).

The 95% kernel and 95 and 100% MCP were used to define the outer home range isopleth. I used cluster analysis to identify the core utilisation area, using nearest neighbour distances within Ranges 6 software (Kenward *et al.* 2003). The analysis assumed that movements during excursive movements inside and outside core areas are different and result in mean distances between locations within range cores being smaller than distances between locations outside of the core. The analysis generates a series of isopleths of diminishing percentage that define increasingly central components of the range. These were graphed to identify discontinuities (Kenward *et al.* 2001) and a 0.1% iteration α-level used to exclude outlying points.

Not all of the calculated home ranges were used for analyses. When exploratory movements resulted in an unusually large home range (i.e. >10 x the average), these were omitted from analyses as the home ranges displayed behaviour that was most likely not associated with parameters measured during the study.

2.2.5. Spatial overlap, interactions and dispersion

Static home range overlap was measured within and between the sexes for annual home ranges. Areal overlap between 95 and 60% kernel isopleths were measured within Arcview 3.3 and percentage overlap calculated using the formula:

$$HR_{1,2}=(A_{1,2}/A_1+A_{1,2}/A_2)/2$$

where $HR_{1,2}$ is the average proportion overlap between cats, $A_{1,2}$ is the area of overlap and A_1 and A_2 is the home range size of animals 1 and 2. To quantify the number of cats that had ranges that could potentially overlap. I measured the distance between the arithmetic mean home range centre of all males and females. The pairs were assumed to be capable of overlapping when pairs of home range centres were within the diameter of the average male or female mean annual home range size, assuming a circular home range. The diameter of the average annual home range size was 11.22km for males and 5.42km for females.

A dynamic overlap test was carried out using Ranges 6 for cats with overlapping home ranges. The geometric mean of observed and random distances between pairs of cat locations, taken on the same day, were compared using the Jacobs's index (Sc), which varies from -1 (strong avoidance) to +1 (strong association); a value of zero indicates that paired locations were positioned randomly in relation to each other (Jacobs 1974). To test the significance of attraction or avoidance between same-sex and between-sex pairs, the values of Jacobs's index were compared with zero using a 1-sample *t*-test.

2.2.6. Factors affecting home range size

The effect of year (2005/6 or 2006/7), sex and season on 95% kernel home ranges (Ln transformed) were analysed using general linear models (GLM) using

cat identity as a random factor in models. Since prey density was significantly higher in summer than winter (Chapter 3), season was also used as a surrogate for the potential effect of prey availability. Effect sizes were assessed using Omega squared values.

To understand the effect of landscape configuration and prey availability on home range size I quantified habitat configuration within sampling circles in each seasonal home range area. Habitat metrics were measured within concentric sampling circles with radii of 500, 1000, 2000 and 3000m from the arithmetic mean home range centre using Fragstats (Mcgarigal & Marks 1995). The metrics measured were chosen for their biological relevance and for their independence from other variables (Table 2.2), they included: mean patch area, percent cover, edge density, habitat connectivity and the season specific prey biomass in preferred habitats (rocky hillslope, mountain steppe and ravine; Chapter 4). Sampling circles were used in preference to home range areas because I found that some variables were correlated with area and therefore would not be independent of home range size. The concentric circle method had no direct relationship with home range size and so independently represented factors available within and surrounding the home range area.

Table 2.2: Environmental variables measured within concentric circles emanating from the centre of Pallas's cat home ranges.

Variables	Description
HR	95% kernel home range area (Ln transformed)
BIOMASS	Prey biomass (kg/ha) available in used habitats (rocky hillslope, mountain steppe and ravine; Ross, 2009)
RH_MPS	Mean patch area (ha) of rocky hillslope patches
%RAV	Percentage cover of ravine habitat
%STEPPE	Percentage cover of steppe habitat
RH_CONNECT	Index of connectivity of rocky hillslope habitat using 200m as a threshold distance of fragmentation; lower values indicate more fragmented habitat

I used linear mixed models to explore the effect of habitat configuration and prey biomass on seasonal 95% kernel home range size (Ln transformed). Cat identity was included as a random factor in models to control for the effect of identity on fixed effects. Year and season were used in models as repeated observations.

Models were run using habitat configuration covariates calculated within each radii from home range centres (500 to 3000m) to predict home range size. An information theoretic approach was used, where models were ranked at each radii scale using Akaike's information criterion adjusted for small sample size (AICc) and candidate models defined *a priori* (Burnham and Anderson 2002; Table 2.3). I examined a correlation matrix of covariates, and only orthogonal variables were combined within models. As correlation was very common between variables, all models were by necessity simple and defined according to five contexts: (i) the 'prey availability' model used an estimate of available prey biomass (BIOMASS) within habitats commonly used by Pallas's cats; (ii) the 'safe' model described the density and distribution of habitats that provided Pallas's cats with the best cover (see Results). The percentage of ravine habitat (%RAVINE) was included as an indicator of safe connections between habitats and as a proxy for mountainous habitat because ravines were most common where surface runoff occurred. Rocky hillslope mean patch size (RH_MPS) was included to indicate rocky hillslope availability and size; (iii) the 'open habitat' model reflected the dominance of open and exposed steppe habitats with poor cover from predators (%STEPPE); (iv) the 'connectivity' model highlighted the connectivity of rocky hillslope (RH_CONNECT), habitats providing good cover and reflecting the feasibility of traversing an area while maintaining close proximity to cover; and (v) the 'null' model contained the random effects (cat identity) but no fixed effects, representing a baseline from which fixed effects could be compared.

Model fit was checked graphically by examining the standardized residuals and case leverage. The ability of models to predict variation in home range size was assessed using Akaike's Information Criteria for small sample sizes (AICc) and the relative weight of evidence for each candidate model was calculated using Akaike's weights (AICw). The statistical significance of explanatory variables to predict home range size was assessed using the *F*-ratio.

Table 2.3: *A priori* models, model variables and hypothesized effect of model on home range size.

Model	Variables	Hypotheses (H1)
Prey availability	BIOMASS	Higher prey availability results in smaller home ranges
Safe	%RAVINE+RH_MPS	Good coverage of safe habitats close to the home range centre inhibits home range expansion
Open habitat	%STEPPE	More open habitat close to the home range centre elicits home range expansion
Connectivity	RH_CONNECT	Higher connectivity of safe habitat results in opportunistic home range expansion

2.3. Results

Of the 29 radio-collared Pallas's cats (Table 2.4), at least one seasonal home range could be calculated for 25 cats. The average (±SE) number of locations used per annual home range was 80.4±2.5 locations and seasonal home ranges were calculated using an average of 42.5±1.3 locations. Home range asymptotes were generally reached at between 30 and 40 fixes (Figure 2.1). Home ranges were not calculated for cats with less than 35 fixes.

Table 2.4: Summary details of radio-collared Pallas's cats.

Cat ID	Sex	Date tracked	Fixes	Comments
8	M	22-Apr-05 to 24-Jun-06	90	Late disperser
3	M	1-May-05 to 4-Apr-06	95	Late disperser
M14	M	22-May-05 to 14-Jun-05	7	Died (body condition suggested disease caused death)
M21	M	14-Feb-06 to 16-Mar-06	9	Predated by raptor
19	M	10-Aug-06 to 29-Nov-06	30	Collar failure
M37	M	28-Mar-07 to 16-Sep-06	51	Late disperser
50	M	7-Oct-06 to 9-Nov-07	97	n/a
44	M	14-Dec-06 to 7-Nov-07	63	n/a
52	M	21-Dec-06 to 10-Nov-07	73	n/a
62	M	8-Jan-07 to 5-Nov-07	66	Late disperser
64	M	10-Jan-07 to 10-Nov-07	70	n/a
60	M	2-Feb-07 to 10-Nov-07	75	Late disperser
54	M	9-Mar-07 to 10-Nov-07	65	n/a
12	F	26-Apr-05 to 22-Nov-05	58	Late disperser
33	F	9-Oct-05 to 7-Nov-07	188	n/a
13	F	8-Dec-05 to 24-Feb-07	108	Predated by raptor
46	F	11-Dec-05 to 2-Nov-07	179	n/a
231	F	25-Jan-06 to 27-Feb-07	9	Predated by red fox
29	F	26-Jan-06 to 26-Aug-06	58	Predated by raptor
272	F	13-Feb-06 to 15-Apr-06	20	Shot by local
35	F	27-Mar-06 to 29-Sep-06	54	Late disperser
23	F	29-Mar-06 to 25-Oct-07	139	Late disperser
21	F	29-Mar-06 to 22-Aug-06	44	Late disperser
14	F	6-Aug-06 to 4-Nov-07	97	n/a
27	F	8-Aug-06 to 2-Oct-07	80	n/a
48	F	24-Aug-06 to 3-Sep-06	6	Collar failure
11	F	14-Aug-06 to 2-Nov-07	106	n/a
37	F	16-Sep-06 to 29-Oct-07	80	Late disperser
42	F	26-Nov-06 to 7-Nov-07	87	n/a

2.3.1. Radio-location error

Radio-tracking error measured as the median deviation between estimated and the real locations of transmitters ±SE was 71.0±10.3m (n=31), at a mean bearing distance of 436m (n=99). The mean areal error (95% confidence circle) for telemetry locations was 1.04 ha. The areal error was sufficiently small, compared with the size of habitat patches in the study area, to make potential bias in location estimates unlikely (Nams 1989). Particular care was taken to ensure accuracy when the Pallas's cat was believed to be using ravines, which had the smallest patch size of the available habitats.

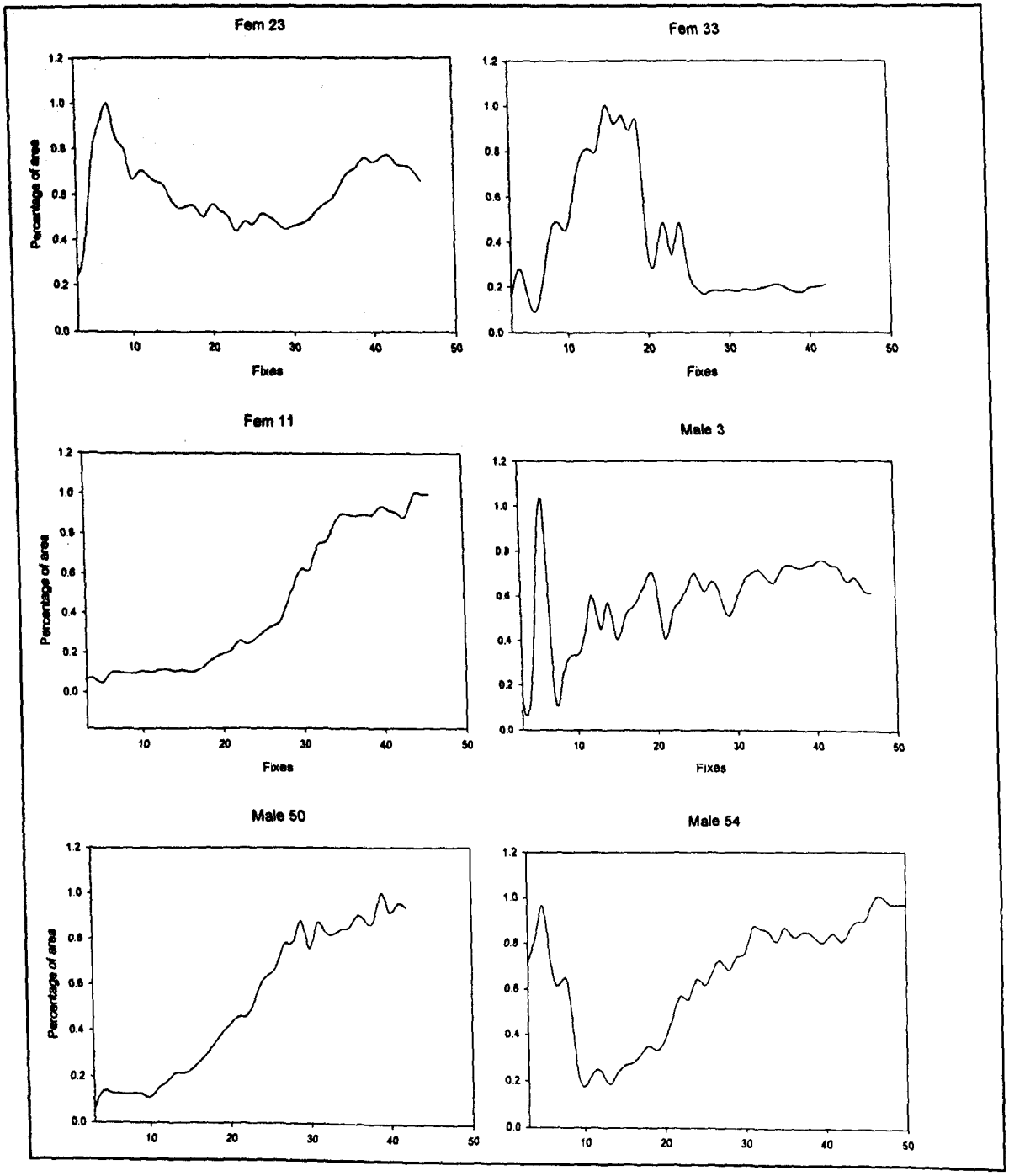

Figure 2.1: Home range asymptote plots of (home range area vs. fixes), using 95 kernel home range estimates with LSCV.

2.3.2. *Home range size*

Male annual home range size (kernel 95) varied from 21 to 207km^2 (mean 98.8±17.2km^2). Female annual home range size varied from 7.4 to 125.2km^2 (mean 23.1±8.9km^2). Incremental cluster polygons indicated that core areas were

most prominent using 60% of locations; male annual 60% core areas varied from 5.7 to 50.3km^2 (mean 16.8±5.6km^2) and female annual 60% core areas varied from 1.3 to 22.0km^2 (mean 4.2±1.5km^2; Table 2.5).

Table 2.5: The mean seasonal and annual home range size (km^2) ±SE for males and females expressed using kernel and MCP estimators.

sex/season		Male summer	Male winter	Male annual	Female summer	Female winter	Female annual
n		9	7	9	16	10	13
Kernel	95	137.5±81.8	48.8±5.7	98.8±17.2	21.8±9.2	14.9±3.4	23.1±8.9
	90	87.2±48.2	36.0±4.6	74.0±13.4	15.0±6.1	11.1±2.6	14.9±5.2
	60	24.0±13.5	11.7±1.3	16.8±5.6	4.4±1.9	3.3±0.7	4.2±1.5
	50	17.4±10.4	8.3±0.9	13.0±4.3	3.2±1.4	2.2±0.5	3.0±1.2
MCP	100	152.5±222.8	47.5±12.9	159.0±59.3	32.2±13.8	16.6±4.6	64.1±18.6
	95	45.7±12.4	38.1±12.7	145.6±69.9	18.7±8.5	10.7±2.5	33.4±12.3
	60	12.4±4.8	14.3±5.6	17.7±3.0	4.2±1.4	2.9±0.6	4.9±1.3

2.3.3. Interactions between Pallas's cats

Males within range of other males were more likely to have overlapping home ranges than females. Of 22 male pairs, 13 were close enough to each other that home range overlap was deemed feasible and 11 (85%) actually overlapped. Of a total of 49 female pairs, 11 were close enough to overlap; 2 (18%) actually overlapped.

In terms of the degree of overlap, male-male 95% kernels had a maximum overlap of 52.3% and an average of 25.4% (n=11 pairs), 60% kernels had a maximum overlap of 44.3% and an average of 9.5% (Table 2.6). The two female pairs that overlapped had a mean 95% kernel overlap of 23.5%, and 60% kernel overlap of 8.2%.

Male home ranges overlapped on average 2.7 (1 to 4) known females, suggesting a polygamous breeding system. Three male home ranges overlapped the same two females on an annual basis and overlap was sustained throughout the breeding season. Of 6 males seen up close during the breeding season, 3 had injuries such as scratch marks on the face and ears and puncture wounds on the

body and tail, suggesting aggressive encounters took place between males vying for access to females.

While static overlap was apparent between males, there was no dynamic interaction of space and the coefficient of sociality (Sc) was not significantly different from zero (t=0.21, p=0.84), suggesting that simultaneous locations were placed randomly in relation to one another, to showing mild avoidance in some cases (Table 2.6). Male-female interactions showed moderate to strong attraction between two separate pairs, but overall Sc was not significantly different from zero (t=1.41, p=0.19).

Table 2.6: The percentage home range overlap for annual home ranges using the 95 and 60% kernel polygons. Dynamic interactions are indicated by the coefficient of sociality between consecutive pairs of points, where -1=strong avoidance, +1=strong association and 0=random, and the geometric mean distance between paired fixes (m).

Sex of Pairs	Pair ID	Overlap (95% kernel)	Overlap (60% kernel)	Coefficient of Sociality (Sc)	Distance between pairs (m)
M-M	50-60	52.30%	0.00%	-0.07	6036
M-M	50-44	20.50%	18.70%	0.04	5529
M-M	50-52	12.10%	0.00%	0.20	6567
M-M	52-60	36.80%	0.00%	-0.09	5775
M-M	54-50	31.50%	44.30%	-0.11	4516
M-M	54-60	10.10%	0.00%	0.03	7677
M-M	54-44	52.20%	41.10%	0.00	5011
M-M	60-44	3.60%	0.00%	0.02	12070
M-M	62-44	15.80%	0.00%	0.06	8878
M-M	62-50	28.80%	0.00%	-0.01	6636
M-M	62-60	15.40%	0.00%	-0.01	8481
F-F	23-37	30.00%	15.90%	0.03	2239
F-F	13-46	17.00%	0.40%	0.07	4617
M-F	44-37	55.64%	0.00%	-0.04	5849
M-F	44-23	29.00%	0.00%	-0.02	5808
M-F	50-11	15.17%	0.00%	0.13	4481
M-F	50-42	9.80%	0.00%	0.01	5092
M-F	52-11	66.13%	39.01%	-0.07	2864
M-F	52-42	18.94%	0.00%	0.22	5817
M-F	60-11	41.90%	18.30%	0.34	2280
M-F	60-42	53.10%	52.60%	0.13	2585
M-F	64-14	14.42%	0.00%	-0.06	5075
M-F	64-46	19.67%	0.00%	0.02	3499
M-F	64-13	23.00%	2.90%	-0.04	3573

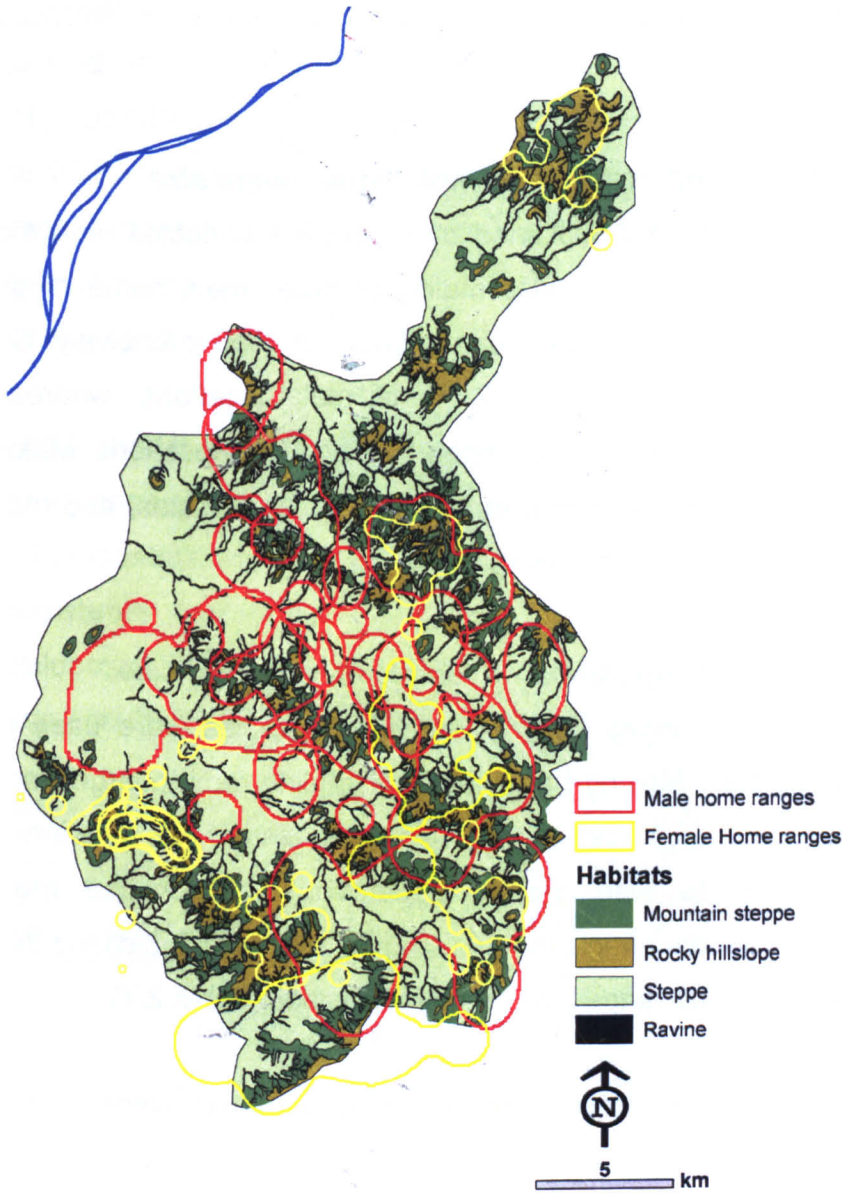

Figure 2.2: Male (red) and female (yellow) 95% kernel isopleths for the winter season of 2006 to 2007 calculated using LSCV.

2.3.4. The effects of year, season and sex on home range size

There were too few male samples to test the effect of year on male home range size, but GLMs showed no effect of year on female home range size ($F_{1,15}$=0.60, p=0.45, ω^2=0.05). There was no effect of season on male ($F_{1,10}$=1.49, p=0.27, ω^2=0.23) or female ($F_{1,15}$=0.42, p=0.52, ω^2=0.04) home range size. Male home ranges were significantly larger than females seasonally ($F_{1,25}$=15.66, p<0.005, ω^2=0.37) and annually ($F_{1,22}$=12.87, p=0.001, ω^2=0.39), with male home ranges 4

to 5 times larger than those of females. The largest male-female differences occurred during winter.

2.3.5. The effects of habitat configuration on male home range size

Male home range size was not well explained by landscape variables, and the models had little interpretive value. This was mainly because male home range size was very large, and so the home range centre was not used intensively. On average, 1000m radii overlapped only 8.7±2.4% of male locations, whereas 1000m radii within female home ranges overlapped 51.5±7.0% of locations. Males therefore spent less time close to the home range centre than females, and radii thus bear little relationship to factors describing the home range.

2.3.6. The effects of habitat configuration on female home range size

A total of 24 seasonal home ranges from 14 individual females were used to model female home range size. Moving from smaller sampling radii to larger radii there was a trend of random effects (cat identity) to explain less of the variation in home range size. There was also greater separation between the most parsimonious and the null random effects model using smaller radii, indicating that larger radii better explained home range size than smaller radii (Table 2.7).

The top two models at the 500m radii scale, 'open' and 'safe habitat', were within 2 AIC of the null, random effects only model, indicating covariates added little to model parsimony. At the 1000m scale the top models were beyond 2 AIC from the null model; the 'safe habitat' model was the most parsimonious, but differed only slightly from the second ranked 'Open' model. Covariates indicated greater coverage of ravines (a proxy for mountainous habitat) and larger mean patch size of rocky hillslope habitat were significantly associated with smaller home ranges, and that greater coverage of open-steppe habitat was significantly associated with larger home ranges. The models supported *a priori* hypotheses that good coverage of safe habitat in the home range centre encourages smaller home range size and greater coverage of open, risky habitats in the home range centre induce home range expansion. The 'connectivity' model was the most parsimonious at 2000 and 3000m scales and high AIC weight values indicated its dominance over other models. The connectivity model suggested that higher

connectivity of safe rocky hillslope habitat in the outer regions of home ranges resulted in opportunistic home range expansion. The sign change of the RH_CONNECT coefficient from negative to positive between the 500-1000m and the 2000-3000m scales suggested a threshold, where good connectivity in the home range core area was associated with small home ranges, and good connectivity in the outer regions of the home range was associated with larger home ranges.

A priori model rankings generally indicated that the 'connectivity' model explained home range size better than other models, although the 'safe' and 'open' models had reasonable predictive capacity within 1000m radii. The 'prey availability' model consistently performed least well; the preference of Pallas's cats for rocky hillslopes (Chapter 4), which had relatively low prey biomass (Chapter 3), may have contributed to the model's poor performance.

Table 2.7: The top explanatory models for ln female home range size, using variables measured in concentric circles from the home range centre at 4 radii, showing the top two models for each radii and the β coefficients ± SE for model variables, where * and ** indicate significance at $p<0.05$ and $p<0.005$. Also showing the variance due to random effects (cat identity), model intercept, ΔAICc corrected for small sample size, ΔAICc from the 'null' random effects only model and AICw to indicate the relative weight of evidence of each model.

Radii	500m		1000m		2000m		3000m	
Model rank	1	2	1	2	1	2	1	2
A priori model	Open	Safe habitat	Safe habitat	Open	Connect	Open	Connect	Safe habitat
Covariates								
Biomass								
Steppe %				0.96±0.07*		0.70±0.89		
Ravine %		-7.98±0.59	-5.97±2.00*					-6.09±5.56
RH MPS		-0.01±0.00	-0.03±0.00*					0.05±0.01**
RH connect	0.53±0.01*				0.45±0.00**		2.51±0.58**	
Random effects - cat identity	0.21±0.00	0.25±0.11	0.20±0.08	0.17±0.00	0.12±0.00	0.17±0.10	0.07±0.00	0.00±0.00
Intercept	6.79±0.18**	7.54±0.22**	7.69±0.22**	6.86±0.17**	4.92±0.12**	6.72±0.49**	4.42±0.63**	6.36±0.37**
AICc	55.48	56.2	54.97	55.11	49.16	56.19	46.34	51.84
ΔAICc null	0.95	0.22	7.42	7.28	8.54	1.52	10.1	4.56
AICw	0.43	0.3	0.49	0.45	0.93	0.03	0.92	0.06

2.4. Discussion

Pallas's cats maintained very large home range areas in comparison to predictions based on body mass. Using the formula described by Lindstedt *et al.* (1986),

Pallas's cat home range size is predicted as 15.15 km^2. Using the predictions of Jetz *et al.* (2004), who based their formula on a much larger sample size (n=70), Pallas's cats' predicted home range size is 2.75 km^2. Both formulas predict substantially smaller home ranges than the observed 100% MCP values. The more robust formula of Jetz *et al.* (2004) indicates the level of deviation from body mass based predictions. The main determinants of individual variation in home range size appeared to be sex and, within females, the degree to which preferred habitats were connected and the amount of preferred habitat within the home range core area. Neither prey biomass nor season had a significant effect on home range size.

2.4.1. Are there spatial associations between Pallas's cats?

Male home ranges overlapped those of several females and, along with observations of males mating with several females, indicated a polygamous mating system. Under polygamy, females select home ranges based on resources, whereas males establish home ranges in relation to the presence of females (Clutton-Brock 1989; Sandell 1989). As males mated with several females, the sparse distribution of females may have been a reason for males having ranges 4-5 times larger than females. The distribution of females may also be a determinant of variability in male home range size, but testing this would require substantially larger sample sizes.

Other than polygamy, there was no obvious social structure indicated by space use. Male home range boundaries and core areas were not exclusive from other males, and there were no dynamic interactions (avoidance or attraction) between adjacent male pairs. Both patterns suggested a lack of territoriality between males, thus differing from other carnivores where territoriality plays a role in population regulation (Baily 1974; Fuller 1989; Poole 1995; Pierce *et al.* 2000). Observations of males with injuries such as bites and scratches during the mating period suggest that males had an *ad hoc* mating strategy, where females within their range were pursued as mates whether or not other males were vying for the same female. In contrast females were not observed with fighting injuries. The lack of territoriality found in males may be associated with their large home ranges, making maintenance of boundaries difficult (Buskirk 2004). Alternatively, the

unpredictability of food or weather patterns in the study area could have made exclusive home ranges impractical because resources outside the home range may be needed in the future (Davies & Houston 1984).

Females did not have such overlapping ranges, though as two pairs of females did overlap, exclusivity was not a rule. However, rather than a territorial explanation of exclusivity, this was most likely an aspect of the low density and the patchy nature of selected habitats in the study area. Pallas's cat density was 4-8 cats/100km^2 (Appendix 2), which translates into a low probability of home range overlap considering female home range size. Additionally, the patchy nature of selected habitats meant that areas of preferred habitat were surrounded by less attractive habitat, creating a natural spacing mechanism. Consequently I postulate that female Pallas's cats' spacing mimicked the spacing patterns of the landscape features on which they depend.

2.4.2. Is prey availability a major determinant of home range size?

While prey is of undoubted importance to carnivores, few studies have demonstrated relationships between home range size and prey abundance (e.g. Grigione *et al.* 2002; Herfindal *et al.* 2005). Prey was one of the poorest explanatory variables of Pallas's cat home range size and, despite dramatic differences in prey availability between summer and winter, season did not have a significant influence on home range size.

2.4.3. Does habitat configuration influence of home range size?

Male home range size was not explained by the metrics measured within radii. As well as home ranges being larger and locations being more dispersed, males spent more time in the outer regions of the home range than females. These behaviours contributed to the failure of models to answer questions regarding the influence of habitat configuration on home range size.

In contrast female home range size was well predicted by habitat configuration. Higher connectivity of rocky hillslopes in the outer regions of the home range was associated with larger female home ranges. Rocky hillslopes are highly selected by female Pallas's cats and provided them with good cover from predators

(Chapter 4). Thus, given safe, connected access routes, females opportunistically explore and expand their home range area. This may minimise the probability of prey depletion or reduce the potential costs of displacement by incoming predators and demonstrates the influence of resource connectivity on spatial patterns. An alternative, though weaker, explanation of female home range size was provided by variables measured close to the home range centre, where good coverage of preferred mountainous and rocky habitats were associated with smaller home ranges. As home ranges exist because of the pull of core resources that are 'known' by the occupant (Börger *et al.* 2008; Van Moorter *et al.* 2009), having the necessary habitat resources in the home range centre was expected to reduce home range size. Although the use of large home ranges may be an important strategy for animals in unpredictable environments, moving outside familiar core areas is comparatively more risky and energetically costly than staying close to a known area (Mitchell & Powell 2004).

2.4.4. Conclusion

I have shown that Pallas's cat home range size is a function of sex and for females is partially explained by habitat configuration. My results suggest that the quality and quantity of resources within the core area influence a female's need to extend its home range area. However, the provision of safe habitats rather than prey resources appeared to be the main factor affecting home range size. The connectivity of preferred habitats in the outer home range was associated with opportunistic home range expansion. The expansionist paradigm may be associated with the uncertainty of a Pallas's cat's resource base, requiring exploration for new, available resources.

My study indicated the relative importance of different ecological factors on the spatial behaviour of a small carnivore. In particular I highlight the potential role of habitat configuration, especially the availability of safe habitats, in determining small carnivore spatial behaviour. I argue that the greater influence of habitat configuration on home range size was a consequence of a trade-off between accessing prey and maintaining cover from predators. If true, the large home range size of Pallas's cats may also be a consequence of anti-predator behaviour, where the avoidance of high risk habitats is compensated for by increasing home

range area. The results also suggest the potential role of small scale behaviours in influencing large scale processes.

My research also suggests that while accessing prey is of undoubted importance to carnivore behaviour, there are strategic differences between small and large carnivores due to their differing energy requirements (Carbone et al. 2007). I postulate that the influence of prey on carnivore home range size should decrease as body size decreases because: (i) small carnivore prey are numerous and more evenly dispersed, and are unable to move large distances, so are unlikely to influence small carnivore space use to the degree that large carnivores are affected; and (ii) small carnivores are more subject to interference competition than large carnivores and, when the risk of predation is high, prey availability may become a secondary priority. Under these conditions the relative importance of habitat properties and partitioning increase as a determinant of small carnivore fitness, whereby habitat configuration becomes a better predictor of space use than prey availability.

Overall, Pallas's cats had very large home range requirements and as a consequence may be challenging to protect within reserves (Woodroffe & Ginsberg 1998), only very large reserves will be capable of accommodating intact populations. Their large spatial requirements may also result in relatively larger impacts due to habitat fragmentation (Haskell *et al.* 2002). In addition, considering that natural habitat fragmentation appeared to have an area restricting effect on Pallas's cat movements, anthropogenic fragmentation is likely to have a similar effect, and thus could restrict Pallas's cats' ability to expand their home range area to counter natural environmental fluctuations or potential displacement by sympatric carnivores. Overall, anthropogenic fragmentation could have substantial negative effects on population viability.

My study has outlined a new and potentially productive area of research for carnivores. Given the relative ease in which landscape data can now be analysed, the potential role of habitat configuration within landscapes provides a new opportunity to advance our understanding of carnivore spatial patterns.

Chapter 3

Dietary niche plasticity of Pallas's cat

Summary

- The degree of niche plasticity can contribute towards a species vulnerability to extinction. In this chapter I explore dietary plasticity and diet composition of Pallas's cat.
- I used faeces collected in latrines from known Pallas's cats, and so was able to analyse sex, season and individual differences.
- Rather than simply measuring the contribution of different prey items to the diet of Pallas's cats, I measured the degree of dietary specialisation by testing prey use against prey availability using compositional analyses.
- Pallas's cats specialise on pika during periods of high and low prey biomass, but take a broad range of other prey species. Pikas are an optimal prey item in terms of energy gain per unit foraging.
- Pika eradication programmes in China and Mongolia pose a serious threat to Pallas's cat. The reduction in pika numbers could result in an energy deficit for Pallas's cat because there are no other species that fill the pika's niche in terms of size and year-round activity.

3.1. Introduction

Numerous ecological characteristics have been related to a species' risk of extinction. One of the most commonly cited factors is the degree of habitat or dietary specialisation (McKinney 1997; Owens & Bennett 2000; Purvis *et al.* 2000). Whilst specialisation allows sympatric species to avoid competition, it also leads to an increased dependence on specific resources, thereby resulting in less flexibility to changes in the resource base (Begon *et al.* 1996).

Optimal foraging theory predicts dietary specialisation. When resources are abundant, optimal foragers should concentrate on their most favoured prey; as resource abundance declines, specialists should expand their diet to include less favoured items. Optimal foragers are therefore specialists when resources are abundant and generalists when resources are scarce (Pyke *et al.* 1977, Dill 1983; Stephens & Krebs 1986; Robinson & Wilson 1998). Dietary specialisation may increase feeding efficiency as the costs of generalisation tend to be comparatively high, since different food groups have different foraging costs and nutritional benefits. Specialisation may also reduce dietary overlap and interspecific competition (MacArthur & Pianka 1966; Fox & Morrow 1981; Futuyma & Moreno 1988; Van Tienderen 1991). The apparent advantages of specialisation are countered by distinct disadvantages. A major functional difference between the two feeding strategies is that generalists are more plastic in their behaviour than specialists, and may more readily switch among foraging strategies (O'Donoghue *et al.* 1998). Thus dietary specialisation may relate to extinction risk because specialists are more sensitive to the loss of specific prey items through human or natural environmental disturbances (Laurence 1991; Sierro & Arlettaz 1997). Indeed, reviews of species extinctions have argued that specialisation is the most fundamental concept in theories of extinction risk (McKinney 1997; McKinney & Lockwood 1999), and so the specialist and generalist concepts can aid understanding of a predators' extinction vulnerability. As there is a history of small mammal control and extermination programmes within the Pallas's cat's range in Mongolia and China (Smith *et al.* 1990 Smith & Foggin 1999), it is important to understand the breadth of their feeding niche so that the impact of changes in their prey base can be assessed.

A review of Pallas's cat ecology in the former USSR, based on eight opportunistic observations (Heptner & Sludski 1992), indicated that pikas were an important food item but that rodents, birds and young marmots were also eaten. Whilst this suggests a relatively broad diet, this needs to be confirmed by a quantified study, coupled with an understanding of prey availability. Theory predicts a generalist strategy where there is a high degree of seasonal variation or unpredictable prey base. As both conditions occurred in the study area, generalisation was the

expected strategy.

My main aim was to understand the potential sensitivity of Pallas's cats to anthropogenic disturbances to their prey base caused by small mammal control programmes. I first tested the prediction that the Pallas's cat is a generalist feeder by quantifying the diet of male and female Pallas's cats in proportion to the availability of prey species, thereby measuring prey selection. I also quantified seasonal variation in the use of prey items and dietary diversity, as measures of dietary plasticity. Quantifying prey selection and plasticity enables a better understanding of how the feeding ecology of Pallas's cat disposes it to current conservation threats.

3.2. Methods

3.2.1. Scat collection and storage

Fresh faeces were collected between July 2006 and November 2007 from latrines outside the dens of radio-collared Pallas's cats. This allowed a positive species identification, identification of the age of the scat to within a week and the sex and identity of the Pallas's cat. Winter and summer diets were considered separately; samples collected within 10 days of the seasonal boundaries were not used in the analyses. All scat samples were field dried outside or next to a fire stove. On return to Bristol, scats were held in a -20°C freezer, except for a 7-day period when samples were placed in a -80°C freezer to kill *Echinococcus* eggs, which are destroyed at temperatures below -70°C (Hildreth *et al.* 2004).

3.2.2. Scat analyses

Faeces were oven dried at 60°C until a constant weight was achieved. Faecal volume was measured by displacement in a water-filled measuring cylinder and the sample left to soak in water and detergent for 2-3 days before being passed through a 5µm sieve. The microscopic fraction (henceforth the micro-fraction) that washed through the sieve was collected and left to sediment for 2 days, the water

decanted off and the sediment left to dry to constant weight in an oven and weighed to the nearest 0.01g. The macroscopic fraction (henceforth the macro-fraction) retained in the sieve was spread in a white tray under water and separated into bones, teeth, skull, feather, arthropod remains and guard hairs of different length and colour. Hair of the same type often remained together, making separation easier. The macro-fraction was oven dried before further inspection.

To aid identification, a reference collection of small mammal skulls, teeth, bones and guard hairs was collected from the study area. Small mammal guard hairs were imprinted on a film of nail varnish on a glass microscope slide to provide a reference collection of hair scale patterns. Hair was also mounted whole on slides as a colour reference. Reference skull and teeth were used to identify similar items in scats to the species level.

Guard hairs in the scat were initially separated by eye using colour and morphology and then identified from hair scale patterns in the reference collection. Hair scale patterns generally allow identification to genus (Day 1966); since only one species of each genus was found in the study area, this enabled identification to species. In cases where it was impossible to separate each food type completely, the total dry mass was taken and the proportion of each prey type in the scat estimated by taking a random sample of 50 guard hairs from the tray. This reduced the possibility of overlooking different taxa within scat samples. Bird fragments were identified to family by examination of barbule structure (Day 1966). Insects were identified to Order. All identified portions of the dried sample were then weighed. The micro-fraction was inspected under a binocular microscope at 7-45x magnification; when it consisted of under-hair and fragments of undigested meat, the weight was split into the proportions of items found in the macro-fraction of the scat.

Cumulative diversity (Hk) was plotted against number of scats analysed to determine whether an asymptote had been reached, and therefore whether the diet of Pallas's cats in the study area had been sampled adequately (Magurran 1988).

3.2.3. Hunting tactics

The hunting tactics of Pallas's cats were investigated opportunistically. When a female Pallas's cat was in a maternal den that was visible from a nearby hillslope, and the surroundings did not have too many visual obstructions, the den was observed using a 30x magnification spotting scope. When snow fell and did not immediately blow and drift, the tracks of Pallas's cats were followed and interpreted. Finally, if a Pallas's cat was seen at night during a spotlight survey, it was observed until out of sight.

3.2.4. Prey availability

Rodent surveys were undertaken twice during each season (summer and winter) on fifteen permanently-marked 500m-long randomly-placed line transects. A Sherman live trap (HB Sherman Traps Inc., Tallahassee, Florida) was placed at 10m intervals along the transect (i.e. 50 per transect), pre-baited for 24 hours with a mix of oats, peanut butter and sunflower oil, and set for 48 hours (2 trap nights). Traps were checked a minimum of twice per 24 hours. In winter, woollen covers were put over the traps to insulate rodents from the cold and extra wool laid inside the trap for bedding. Captured animals were dropped into a cloth bag, sexed, weighed and marked on the head with a red marker pen before being released; recaptures were excluded from abundance estimates and factored into the equation (below) as sprung traps.

The survey boundary, indicating the coverage of line transects, was calculated using three 9x9 trapping grids, with 10m trap spacing, in each of the four available habitats. Rodents caught within grids were individually marked and the distance between first capture and recapture calculated. The average habitat-specific recapture distance was then used to delineate the survey boundary either side of the trap-line. Rodent density was calculated by modifying Nelson and Clark's (1973) index of captures per 100 traps by incorporating the survey boundary into calculations, rodent density was calculated as:

$$\text{rodents/ha}=(A \times 100/TU) \times (S \times L/10{,}000)$$

where *A*=number of small mammals caught, TU=*P* x *I* x *N* (trapping units corrected for sprung traps), *P*=number of trapping intervals, *I*=length of trapping interval, *N*=number of traps, *S*=survey boundary (m), *L*=length of transect (m).

Table 3.1: Average recapture distance (m) ±SE of rodents from the trap of first capture.

Habitat	Steppe	Mountain steppe	Rocky hillslope	Ravine
N	54	35	31	74
average distance (m)	23.0±2.6	22.4±4.0	26.6±3.6	24.6±2.9

As pikas (*Ochotona daurica*) did not consistently enter Sherman traps, pellet group sign surveys along the same transect lines were used to estimate density. Pellet groups in a 10m wide strip centred on the transect line were dispersed with a brush and, 24 hours later, the number of new pellet groups were counted in 10x10m sections corresponding to the trap spacing. Since Afgan pikas (*Ochotona rufescens*) were observed to produce a mean of 4.13 pellet groups during their diurnal activity periods (Matsuzawa *et al.* 1981), it was assumed that each 4.13 pellet groups counted equalled one pika. I used a survey boundary equal to the radius of Daurian pikas 80% home range core areas (32m). As the 80% core area is used during daily activity (Wang *et al.* 2000) it corresponds to the sample period. Pika density was subsequently calculated as:

pika/ha=(*pg*/4.13) x (*S* x *L*/10,000)

where *pg*=pellet groups counted on the transect, *L*=length of transect (m), *S*=survey boundary (m).

3.2.5. Prey biomass

As body mass varied between prey species, biomass provided a more informative measure of prey availability. Density was converted to habitat-specific biomass by multiplying rodent and pika density by the mean mass of the animals captured in each habitat. The total biomass (biomass/ha) for each habitat was the sum of the rodent and pika biomass estimates.

3.2.6. Statistical analyses

Since captive Pallas's cats defecate on average once per day (W. Swanson, pers. comm.), I assumed that the same prey item was only represented in one scat. The importance of each prey type to Pallas's cats was quantified using three methods: percentage occurrence, mass ingested and compositional analyses. Percentage occurrence (PO) was calculated as:

$$POi(\%)=(ni/\sum ni)100$$

where, *ni*=number of scats containing species i.

Percentage occurrence accounts for the presence of multiple prey items in individual scats, whereas frequency of occurrence only indicates presence or absence. Thus percent occurrence indicates the relative frequency with which each item is consumed (Ackerman *et al.* 1984). However, when prey items vary in size, as was the case in this study, frequency indices can distort the relative contribution of each prey item in the diet (Ackerman *et al.* 1984). To overcome this problem, data are also presented as percentage fresh biomass ingested (Mi), calculated as:

$$Mi= C_d \times 100/\sum(m \times C_d)$$

where, Mi=mass of food *i* ingested (g), C_d =coefficient of digestion for food i, *m*=dry mass (g) of food remains *i* in sample (Reynolds & Aebsicher 1991).

Digestion coefficients were obtained from the literature for red foxes (Lockie 1959; Reynolds & Aebischer 1991; Reynolds & Tapper 1995). While digestion is likely to differ slightly between red foxes and Pallas's cats, I was interested in the relative importance of different prey items and assumed that the relative differences in digestion of different prey species eaten by foxes and Pallas's cats would be approximately the same.

Overall differences in the use of prey between sex and season were detected by χ^2 analyses using frequency of occurrence. The analyses were conducted for each food grouping separately to avoid problems associated with non-independence, since each scat sample could contain more than one prey species (Reynolds & Aebischer 1991). *P*-values were adjusted using Bonferroni confidence intervals to control for experiment-wise error of multiple comparisons. Overall differences in frequency of occurrence of prey between sex and season were tested using global one-way analyses of similarities (ANOSIM), based on a Brae-Curtis similarity matrix (Clark & Warwick 2001).

The standardised Levins' index of niche breadth was calculated for sex and seasonal groups as a measure of dietary diversity, using both frequency of occurrence and mass ingested. The index ranges in value from 0 to 1, where 0 denotes dietary specialisation and 1 indicates a generalist pattern (Krebs 1999). Differences in diversity between seasons and sexes were detected using diversity *t*-tests within the programme Past (Hammer *et al.* 2001).

Prey biomass data were analysed using Kruskal-Wallis one-way analysis of variance. I made post-hoc pair-wise comparisons of prey biomass in each habitat using Mann-Whitney U tests with Bonferroni corrections for multiple comparisons.

Prey selection was measured using compositional analyses (Aebischer *et al.* 1993). Selection was only measured for three groups of small mammals: pika, steppe rodents and mountain voles. The groups were representative of size, as pika are 2-3 times the size of rodents, and habitat differences, since mountain voles only utilise rocky areas, whereas all other species are absent from rocky habitats, preferring grassland. Prey utilisation was measured as the proportion of each small mammal group in an individual's diet. Prey availability was calculated by measuring the area of each available habitat within individual Pallas's cats' 95% kernel home-range area (*Hi*) using ArcGIS 9.2. The mean density of each prey category found in each habitat (*pi*) was then multiplied by the area of each habitat in the home range, to give an abundance measure for each prey group. Compositional analysis uses the animal, rather than the individual scat samples,

as the sampling unit (Aebischer *et al.* 1993). To overcome constraints due to limited numbers of scats per individual, individuals with similar proportions of habitats within their home range were combined and the proportional availability of prey was measured in their combined home range areas.

MANOVA linear models were used to analyse the proportion of 'utilised prey' verses the proportion of 'prey availability'. Wilks' λ scores were used to test for departures from random use of the available prey groups. Following a significant MANOVA result ($p<0.05$), I assigned ranks to each prey category using *t*-tests to determine significance (Aebischer *et al.* 1993). For analyses of differences in selection between the sexes, seasonal samples were combined into one sexual grouping; sexes were combined for the analyses of seasonal differences in selection.

3.3. Results

3.3.1. Scat analyses

I analysed 146 scats from 10 male and 12 female Pallas's cats: small mammals formed 82.3% of all items consumed and 93.3% of ingested biomass (Table 3.2). The most frequently consumed small mammals were Daurian pikas, Mongolian gerbils and mountain voles. Daurian hedgehogs (*Mesechinus dauuricus*) and Tolai hares (*Lepus tolai*) were rarely eaten. Birds were relatively unimportant in terms of biomass; most were passerines, with one Daurian partridge (*Perdix daurica*) and one unidentified Falconiforme. Reptiles were scarce in the study area and consumed infrequently. Insects, in particular beetles and grasshoppers, were frequently eaten but represented a small proportion of ingested biomass. Two marmots and domestic livestock were probably consumed as carrion, which was a relatively important winter food source in terms of biomass. Several non-food items were recorded: all scats contained a small amount of Pallas's cat hair from grooming. Ticks from grooming, vegetation ingested incidentally when eating prey, parasitic worms and worm eggs were also recorded.

The cumulative dietary diversity (H_k) started to stabilise at 20 scats and reached an asymptote at c. 70-80 scats (Figure 3.1), indicating that a representative sample had been obtained.

Table 3.2: Prey identified in Pallas's cat scats from the study area, with sex and season groups combined.

Prey Items	*n*	Percentage occurrence (%)	Mass ingested (%)
Small Mammals			
Pika (*Ochotona daurica*)	89	35.7%	53.8%
Mongolian gerbil (*Meriones unguiculatus*)	52	20.9%	16.80%
Mountain vole (*Alticola semicanis*)	41	16.5%	14.0%
Brandt's vole (*Lasiopodomys brandtii*)	14	5.6%	4.4%
Chinese hamster (*Cricetulus barbensis*)	8	3.2%	3.4%
Long-tailed Ground Squirrel (*Spermophilus undulatus*)	1	0.4%	0.9%
Medium sized mammals			
Tolai hare (*Lepus tolai*)	2	0.8%	0.9%
Daurian hedgehog (*Mesechinus dauuricus*)	2	0.8%	0.0%
Reptiles			
Steppe runner (*Eremias strauchi*)	3	1.2%	0.3%
Birds			
Passerines	8	3.2%	0.4%
Galliforms	1	0.4%	0.1%
Falconiformes	1	0.4%	0.1%
Insects			
Coleoptera - beetles	11	4.4%	0.1%
Orthoptera - grasshoppers	12	4.8%	0.5%
Carrion			
Goat, sheep	2	0.8%	1.8%
Marmot	2	0.8%	2.6%
Non-food items, accidental ingestion			
Vegetation	35		
Parasite eggs	35		
Parasitic worms	10		
Ticks	6		
Grooming hairs	146		

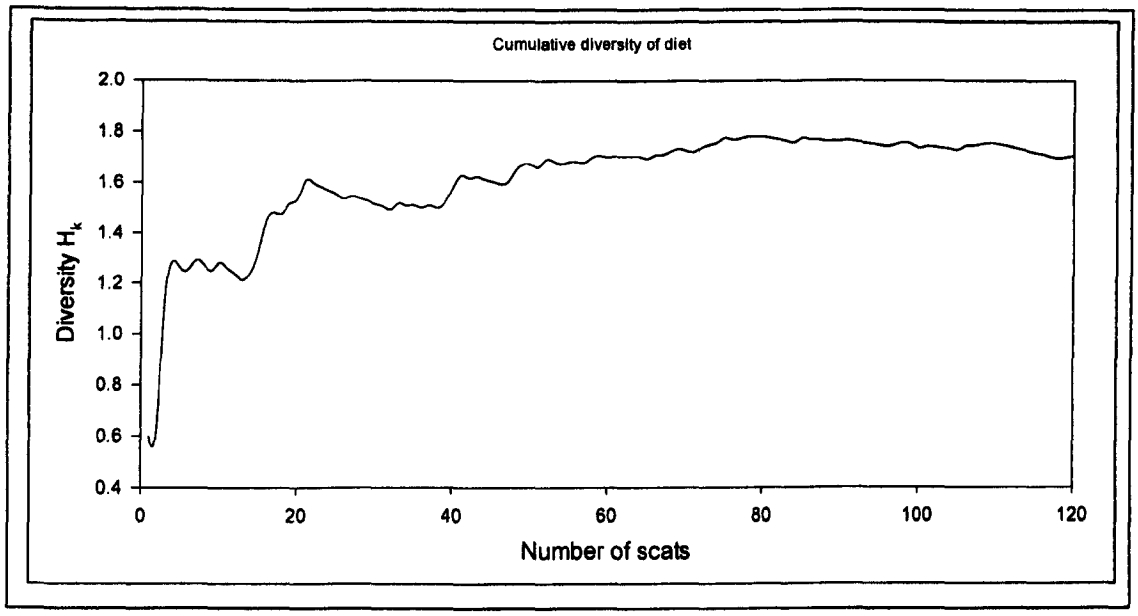

Figure 3.1: Cumulative diversity (H_k) Pallas's cat diet with increasing sample size of scats.

3.3.2. Hunting techniques and behaviour

Three female Pallas's cats were observed for a total of 16 hours during the summer. Twelve sets of Pallas's cat' prints were followed and interpreted during the winter. Pallas's cats used three hunting techniques. 'Stalking' involved creeping slowly and low to the ground, using vegetation or rocks as cover until close enough to pounce on their prey (*n*=4). A 'moving and flushing' technique was used more frequently: the cat would quickly walk through the summer undergrowth flushing and capturing unwary small mammals and birds (*n*=7). This technique is unlikely to be used in the winter since it requires high prey density and good grass cover that limits the prey's ability to anticipate the attack. Instead, signs found in snow suggested an 'ambush' technique was used in winter, where cats waited outside a burrow for prey to emerge before attacking. The 'ambush' technique was only observed outside pika burrows (*n*=3) but prints in the snow indicated that cats' stopped at the burrows of other small mammals, presumably checking occupancy.

Females with kittens took live prey to the maternal den and kittens were observed to 'play hunt' small mammals (*n*=3). Whole uneaten birds were also found outside maternal dens, suggesting that they may have been taken there primarily for the

purpose of learning. While Pallas's cats are typically solitary, when the kittens were 3-4 months old, foraging and presumably hunting occurred as mother-kitten family groups. These family groups (n=2) were only observed soon after sunset but may have occurred during the day as well.

3.3.3. Small mammal abundance and biomass

A total of 2865 individual rodents were captured over 10,106 trap nights. Traps covered similar percentages of habitats as those available in the study area (Table 3.3). Mongolian gerbils formed 67.4% of captures, followed by Chinese striped hamster (14.6%), mountain vole (9.1%), Russian dwarf hamster (4.9%), Brandt's vole (3.6%) and souslik (0.4%). Rodent abundance data were extremely variable owing to the patchy distribution of colonies.

Table 3.3: Habitat coverage of individual traps placed in 15 random line transects, showing total number of traps in each habitat and percentage coverage.

	Steppe	Mountain steppe	Rocky hillslope	Ravine	Total
Number of traps	460	146	117	27	750
% of total	61%	20%	16%	3.6%	

Since prey species had different habitat preferences, the mean rodent body mass available in each habitat was different. The mean body mass of captures also differed between habitats (Table 3.4): t-tests showed that mean rodent body mass within steppe and ravine was not significantly different, but both had larger rodent body mass than mountain steppe and rocky hillslope (p<0.005). Rodent body mass was also greater in rocky hillslope than mountain steppe (p<0.05).

Table 3.4: Mean body mass (g) of rodent captures in different habitats and pika using all captures.

	Steppe	Mountain steppe	Rocky hillslope	Ravine	Pika
Mean body mass (g)	54.5	31.0	35.6	53.1	135.6
n	622	72	116	212	44
SE	0.5	1.7	1.1	0.7	4.1

Rodent biomass was significantly different between habitats during summer

(H_3=14.89, p<0.005) but not winter (H_3=3.28, p=0.36). In summer, steppe had significantly greater rodent biomass than rocky hillslope (p<0.005) and mountain steppe (p=0.007); other habitats were not significantly different. Ravine consistently had the highest rodent biomass, followed by steppe, mountain steppe and rocky hillslope; these trends were consistent between seasons (Tables 3.5 and 3.6). Summer rodent biomass was significantly higher than winter biomass ($U_{1,53}$=191, p=0.005).

Pika biomass differed between habitats in summer (H_3=8.60, p=0.03), but not winter (H_3=3.95, p=0.27). In summer mountain steppe had greater pika biomass than rocky hillslope (p=0.02); other habitats were not significantly different (Table 3.5). There was no significant difference in pika biomass between seasons (U_1= 1767.50, p=0.99).

Table 3.5: Summer mean rodent and pika density (individuals/ha) and biomass (kg/ha) ±SE.

Habitat	Rodent density (rodent/ha) ±SE	Pika density (pika/ha) ±SE	Rodent biomass (kg/ha) ±SE	Pika biomass (kg/ha) ±SE
Steppe	14.03±2.69	0.93±0.25	0.76±0.14	0.13±0.03
Mountain steppe	9.90±1.76	0.74±0.26	0.31±0.05	0.05±0.01
Rocky hillslope	7.09±1.49	0.00±0.00	0.25±0.05	0.00±0.00
Ravine	14.50±4.65	1.31±0.44	0.77±0.25	0.18±0.06

Table 3.6: Winter mean rodent and pika density (individuals/ha) and biomass (kg/ha) ±SE.

Habitat	Rodent density (rodent/ha) ±SE	Pika density (pika/ha) ±SE	Rodent biomass (kg/ha) ±SE	Pika biomass (kg/ha) ±SE
Steppe	2.36±0.73	0.86±0.21	0.10±0.03	0.12±0.03
Mountain steppe	2.07±0.87	0.40±0.11	0.06±0.03	0.05±0.01
Rocky hillslope	1.57±0.52	0.11±0.06	0.06±0.02	0.02±0.01
Ravine	5.47±5.11	0.35±0.13	0.21±0.19	0.05±0.02

3.3.4. Sexual differences in diet selection

Male Pallas's cats use of small mammal prey was disproportional to prey availability within their 95% kernel home range (λ=0.06, p<0.005). Pikas were selected by males (Table 3.7); they were used significantly more than steppe rodents (p=0.006) and mountain voles (p=0.03), and mountain voles were used

significantly more than steppe rodents (p=0.009).

Table 3.7: Mean log-ratios ± SE of differences in prey selection by males for the 3 most frequently selected prey categories; * indicates a significant difference (p<0.05).

	Pika	Steppe rodents	Mountain voles
Pika		2.74±0.51*	1.88±0.56*
Steppe rodents	-2.74±0.51*		-0.87±0.18*
Mountain voles	-1.88±0.56*	0.87±0.18*	

Use of small mammal prey by females was also disproportional to availability within the 95% kernel home range (λ=0.10, p<0.005). As with males, pika were eaten significantly more than steppe rodents (p=0.001) and mountain voles (p<0.001). There were no differences detected between selection of mountain voles and steppe rodents (Table 3.8).

Table 3.8: Mean log-ratios ± SE of differences in prey selection by females for the 3 most frequently selected prey categories; * indicates a significant difference (p<0.05).

	Pika	Steppe rodents	Mountain vole
Pika		3.47±0.65*	2.72±0.48*
Steppe rodents	-3.47±0.65*		-0.75±0.80
Mountain vole	-2.72±0.48*	0.75±0.80	

Males had a higher frequency of occurrence of steppe rodents in scats than females (χ^2=11.55, df=1, p<0.005). Females also consumed insects significantly more frequently than males (χ^2=3.756, df=1, p=0.05). Females had greater dietary diversity than males in winter (t=10.62, p<0.005; Table 3.9), whereas males had greater dietary diversity than females in summer (t=10.48, p<0.005). Although sexual differences in diet were greatest in summer, a global one-way ANOSIM was not significant (R=0.025, p=0.94).

3.3.5. Seasonal variation in diet

Compositional analyses showed that selection for pikas was significantly greater in summer than winter (t=5.82, df=5, p<0.005), whereas steppe rodents were used proportionally more in winter than summer (t=3.28, df=5, p<0.02). However, steppe rodents were used proportionally less than was available in both seasons and so were not selected. There was no difference in selection of mountain voles

between seasons (p<0.49); they were consumed in proportion to availability in both seasons.

Using frequency of occurrence in scats, pika were consumed significantly more frequently in summer than winter (χ^2=8.29, df=1, p<0.005). There was a non-significant trend for insects to be consumed more frequently in winter than summer, despite insects being dead or dormant during the winter.

Dietary diversity differed between seasons, with significantly lower dietary diversity in summer than winter (t=44.68, p<0.005; Table 3.9). The difference in dietary diversity between summer and winter was much greater when the mass of prey ingested was considered. This reflected the dominance of pika in summer and the greater mass of pika in relation to rodents.

Table 3.9: Standardised Levin's index showing dietary diversity of male and female Pallas's cats in summer and winter using (a) percent occurrence (PO) and (b) mass ingested (Mi).

(a) PO	Male	Female
Summer	0.40	0.30
Winter	0.44	0.46

(b) Mi	Male	Female
Summer	0.30	0.15
Winter	0.65	0.65

3.4. Discussion

Pallas's cats used a broad range of food items but small mammals formed the majority of the diet, with pika the most important small mammal. The dietary composition largely confirmed what has already been noted in opportunistic accounts from the former USSR (Heptner & Sludski 1992). Additional items found in this study included insects, carrion, reptiles and a large bird of prey. Only two species of small mammals, Siberian jerboa and Russian dwarf hamsters, were not eaten: both species are nocturnal, suggesting that Pallas's cats do not hunt at night, or at least do so infrequently. This is confirmed by their mainly crepuscular activity patterns (Appendix 1).

Male and female Pallas's cats are not dimorphic in size and there were no dramatic differences in prey use by the sexes, but there were sexual differences in

dietary diversity. Females narrowed their niche and specialised on pika to a greater degree than males during the summer, while in winter females generalised to a greater degree than males. Females therefore showed an extreme case of the foraging mode predicted by optimal foraging theory (MacArthur & Pianka 1966; Stephens & Krebs 1986), where specialisation is increased in the summer to maximise the net rate of energy intake and diet is broadened in winter to survive the 'lean' period.

If prey availability had not been measured, Pallas's cats could easily have been labelled a generalist with a preference for pika. However, Pallas's cats showed strong selection for pika, using them disproportionately to availability in summer and winter. However, during winter both sexes diversified their diet substantially and selected pika significantly less, probably in response to the decreasing availability of all prey species. The strong selection of pika and the functional responses of Pallas's cats to changing prey density are reminiscent of the feeding ecology of the Canadian lynx (*Lynx canadensis*). Lynx are usually considered specialist predators of snowshoe hares (*Lepus americanus*) (Parker *et al.* 1983; O'Donoghue *et al.* 1998). However, their food habits become more opportunistic during periods of low hare density (Koehler & Aubry 1994; O'Donoghue *et al.* 1998). The selection of pika both in this study, and high use of pika in other areas (Heptner & Sludski 1992), alongside the diversification of diet when pika availability is reduced, indicate that Pallas's cats are a facultative specialist predator of pika.

According to diet selection theory, prey selection should be non-random if the intrinsic values of the prey types differ (Stephens & Krebs 1986). The optimisation of energy acquisition appears to explain the specialist pattern displayed by Pallas's cats, as pikas are approximately 2.3 times the size of rodents. Pikas are also slower moving than most available rodents and use distinct trails to move between their nesting burrows. These traits are likely to increase their susceptibility to Pallas's cat predation. Specialisation on pikas therefore most likely optimises their energy intake per unit foraging.

Specialisation is thought to make species more vulnerable to environmental change (McKinney 1997; Harcourt & Coppeto 2002; Boyles & Strom 2007). Although specialisation does increase Pallas's cats' vulnerability, their seasonal increase in dietary diversity and range of hunting techniques demonstrates a degree of dietary flexibility. This facultative ability reduces the potential direct costs of specialisation. Nevertheless, the disappearance of pika could result in an energy deficit in the diet of Pallas's cat, as there are no other species that fill the pikas' niche in terms of size and year-round activity.

The loss of pikas has become a significant issue as they are believed to compete with livestock for forage and are thus regarded as a pest. Large-scale poisoning campaigns designed to control or eliminate pika in China and parts of Mongolia (Smith *et al.* 1990, Smith & Foggin 1999; Clark *et al.* 2006; Smith & Xie 2008) could have serious repercussions for Pallas's cat. At best, the loss of pika would affect fitness and result in a reduction in population density; at worst Pallas's cat could become locally extinct. The conservation of pika populations should therefore be incorporated into any conservation plan for Pallas's cat, particularly where extermination programmes exist.

Chapter 4

Foraging habitat selection by Pallas's cat in relation to limiting factors

Summary

1. An understanding of the resources used by animals is required to determine how those resources affect long-term population persistence.
2. I used resource selection functions to characterise resource use of male and female Pallas's cats in summer and winter and related selection to fitness benefits gained from different habitats by measuring body mass as a proxy for fitness, mortality, cover from predators and prey availability in each habitat.
3. I show that Pallas's cats are habitat specialists, selecting habitats with better cover from predators.
4. Seasonal changes in habitat use could be explained by trade-offs between risk of mortality and obtaining food or reproductive opportunities to enhance fitness.
5. Pallas's cats, particularly males, were attracted or indifferent to the presence of nomad camps. If, as would be expected, mortality increases closer to camps, then camps could be ecological traps.

4.1. Introduction

Habitat selection is generally poorly understood but critical in efforts to preserve threatened species. Habitat selection provides fundamental information about how animals meet their requirements for survival and is a crucial process affecting most components of fitness (Danchin *et al.* 1998; Green & Stamps 2001; Manly *et al.* 2002; Morris 2003). Examining the potential effects of habitat selection on fitness should therefore underpin the definition of a species' habitat (Rettie & Messier 2000) and is essential for evaluating and prioritising areas for conservation.

All animals live under physiological and environmental constraints. Foraging behaviour and habitat selection can show how an animal perceives its environment and overcomes its particular set of constraints (Stephens & Krebs 1986). For example, many morphological defences from predation such as crypsis require animals to restrict themselves to suitable habitats (Caro 2005), but food may be most efficiently gained from another habitat. Habitat selection is then a compromise between the conflicting demands of energy gain and mortality risk (Grand & Dill 1999).

Preferred foraging habitats are often typified as those with the highest prey availability (Huey 1991; Potvin *et al.* 2000) and prey density is a fundamental determinant of carnivore density (Carbone & Gittleman 2002). The preferred habitat of some carnivores is related to the ease of capturing their prey (Powell 1994; Murray *et al.* 1995). However, when a carnivore is itself prey, the need for safety is likely to alter how and where prey is accessed and so patch choice becomes coupled with predation risk. Under these circumstances, habitat selection will reflect a balance between foraging efficiency and cover from predators, resulting in trade-offs between food and safety (Lima & Dill 1990; Brown & Kotler 2004).

Constraints on habitat selection can also be influenced by human activity. Animals may perceive human disturbance in a similar manner to predation risk, responding as they would to encounters with predators (Berger *et al.* 1983; Gill & Sutherland 2000; Frid & Dill 2002). Persecution by people remains the greatest threat to the persistence of many carnivores (Treves & Karanth 2003), particularly the larger species (Woodroffe & Ginsberg 1998). Avoidance of humans can also lead to disturbance-related reductions in habitat availability, detracting from an animal's ability to meet its basic needs (Johnson *et al.* 2005). Alternatively, when humans are not avoided because the risks of interactions have not been learned, encounters can increase mortality.

As Pallas's cats are predated upon and live in an extremely seasonal environment, selective pressures should have resulted in patterns of habitat selection that minimise predation risks and energetic constraints. As a framework for quantifying

the interactions between Pallas's cats, their surrounding habitat and potential disturbances I used radio-telemetry data to formulate resource selection functions, which are widely regarded as the most robust means of measuring habitat selection (Boyce *et al.* 2002; Manly *et al.* 2002; Johnson *et al.* 2006). My primary objective was to develop predictive models describing the response of Pallas's cats to variables representing habitat with differing costs and benefits, including cover from predators and avoidance or use of areas near human settlements.

To understand the costs and benefits derived from habitats I examined two key assumptions: (1) that prey biomass varies between habitats, and (2) that different habitats have different levels of predation risk. Although I could not measure habitat-specific survival or reproductive fitness, these two assumptions were used to assess the potential costs (risk of predation) and benefits (food, safety) obtainable from different habitats. Resource-selection functions with a presence-available design were used to quantify habitat selection by both male and female Pallas's cats in different seasons. Lastly, since season created extreme conditions potentially affecting fitness, I used body mass throughout the year as a proxy of fitness, where relatively high body mass indicated fitness and low body mass indicated poor condition. I used the tests and model predictions to interpret the selection patterns of Pallas's cats in the context of fitness, with the overall aim of assessing the suitability of resources for Pallas's cats and how resources are likely to affect long-term population persistence. I aimed to answer four main questions:

1. Do Pallas's cats select habitat?
2. Do Pallas's cats select habitat with high prey biomass?
3. Does low prey biomass alter habitat selection as Pallas's cats satisfy their need for food at the expense of their need for safety?
4. Do Pallas's cats avoid areas with humans and human disturbances?

4.2. Methods

4.2.1. Habitat use

Radio-tracking was used to assess patterns of habitat use. The majority of radio-locations used were classed as active (86%), indicated by signals with erratic strength and pitch (Nams 1989); locations outside area in which habitats had been mapped were discarded, as were all fixes where Pallas's cats were within dens. All data were pooled and separated by season (summer and winter) and by sex. Pooling between years assumed that habitat availability and use were similar within the study period. This assumption was felt to be valid as, for the duration of the study, there were no measured changes in human population, exploitation in the area (e.g. hunting), or notable weather events.

4.2.2. Mortality

To understand mortality risk, I assessed the cause of mortality of radio-collared cats and conducted informal interviews with local people. On hearing a mortality signal from a radio-collared cat, the body was collected and a necropsy undertaken. When the body was intact, outward signs of injury were assessed and the cat then skinned to examine subcutaneous injuries such as bites or marks inflicted by talons. Bone fractures were recorded and finally the cat was examined internally for obvious injuries or parasites. Other signs used to ascertain the cause of death included tracks and faeces surrounding the body and teeth or talon marks on the radio-collar. Additional records of mortality were collected from nomads within the study area during visits to nomad camps and evidence verified by inspecting the dead cat.

To understand the reaction of Pallas's cats to people, I tested the difference between distance to nomad camps in the summer (when vacant) and winter (when occupied by nomads) using an ANOVA.

4.2.3. Seasonal body mass

To assess the condition of radio-collared cats, I measured body mass throughout the year. Higher body mass was assumed to indicate that cats were in good condition and had sufficient food, while relatively low body mass indicated poor

condition. Body mass was measured to the nearest 125g during all Pallas's cat captures using a Pesola Macro-line spring scale (Pesola AG, Baar, Switzerland), with a 10kg±0.3% capacity. The Pallas's cat was placed inside a hemp sack to be weighed and the mass of the hemp sack and the radio-collar were subtracted afterwards.

4.2.4. Prey biomass in different habitats

Prey availability was measured using habitat and season-specific trapping for rodent species and sign surveys for pika, as described in Chapter 3.

4.2.5. Detection distance and escape potential of habitats

The risks associated with using each habitat were estimated using factors expected to alter the ability of a predator to detect and capture a Pallas's cat. The line of sight cover of each habitat was measured using a life-sized Pallas's cat stuffed toy (Wild Republic, USA). The model cat was placed at randomly-generated coordinates within each of the defined habitats in the study area. I then slowly walked away from the cat and recorded the point at which it could no longer be seen at all 4 cardinal points of the compass. This detection distance was measured at 10 random locations within each of the four habitats at the end of summer (August), with high vegetation biomass, and at the end of winter (March), with the lowest vegetation biomass. The detection distance did not take account of the cat's camouflage ability since the model cat's position was known.

Since detection distance was a measure of the disruptive qualities of a habitat and as these features e.g. rocks, topography, undergrowth and cliffs were used by Pallas's cats to escape predation, detection distance was also a measure of the escape potential of each habitat. Differences in cover were tested by an ANOVA using $\sqrt{}$ transformed data.

4.2.6. Model construction

A used (radio-telemetry fixes) and available (randomly generated points) design was used to construct univariate resource selection ratios and multivariate resource selection functions (Manly *et al.* 2002). The used sample data were

entered into a GIS database and complimentary random available locations were generated using Hawth's analyses tools (Beyer 2004) for ArcGIS 9.2. An order of magnitude greater random available points were generated than those used so that the used locations were a sufficiently small proportion of the possible available locations (Johnson *et al.* 2006). Available points were drawn from two spatial scales:

1) To understand what features Pallas's cats used to select their home ranges, points were generated in all areas of the study area (study area scale).
2) To understand selection at the finer, within home range scale, random points were generated only from within their home ranges (home range scale).

Home range was defined by the 95% kernel method (LSCV) using the animal movement Arcview 3.3 extension (Hooge & Eichenlaub 2000). The random locations generated within each home range area were grouped together as the available sample. Although individual animals were radio-collared, they were not identified in the model.

Habitat covariates were obtained for the used and available samples from a GIS database containing a digitised map (Table 4.1). Selection patterns were also investigated at a fine scale by measuring the habitat proportions (S, MS, RH, Rav) available in circles around points with radii of 50, 100 and 150m.

Table 4.1: A description of the variables used to construct candidate models.

Variable	Type	Description
Dist S	Continuous	Distance (m) to steppe habitat
Dist MS	Continuous	Distance (m) to mountain steppe habitat
Dist RH	Continuous	Distance (m) to rocky hillslope habitat
Dist Rav	Continuous	Distance (m) to the ravine habitat
Cover	Continuous	Minimum straight line distance to rocky hillslope or ravine habitats
Open	Continuous	Minimum straight line distance to steppe or mountain steppe habitats
S50, 100, 150	Continuous	The proportion of steppe habitat within a 50, 100 and 150m circle surrounding the identified point
MS50, 100, 150	Continuous	The proportion of mountain steppe habitat within a 50, 100 and 150m circle surrounding the identified point
RH50, 100, 150	Continuous	The proportion of rocky hillslope habitat within a 50, 100 and 150m circle surrounding the identified point
Rav50, 100, 150	Continuous	The proportion of ravine habitat within a 50, 100 and 150m circle surrounding the identified point
Slope	Continuous	The slope (°) at the identified point
Elevation	Continuous	Elevation above sea level (m) at the identified point
Solar radiation Index	Continuous	Index of solar intensity (Keating *et al.* 2007)

4.2.7. Univariate analyses

Resource selection ratios were constructed for each variable to identify the most important predictors of Pallas's cat presence and to aid interpretation of selection patterns. All variables were first converted into to categorical variables and the selection ratio for a given resource category calculated as the proportion used relative to the proportion available. Selection ratios greater than 1 indicate selection, equal to 1 random use and less than 1 avoidance (Manly *et al.* 2002):

$$w_i = o_i / \pi_i$$

where w_i is an estimate of resource selection, o_i is the proportion of locations used by Pallas's cats in the *i*th type, and π_i is the proportion available for randomly generated locations. Because of multiple comparisons, Bonferroni *Z* corrections were used to calculate 95% confidence intervals (CI) using the formula:

$$Z_{\alpha/2k}\sqrt{[o_i\,(1 - o_i)/(U_+\pi_i^2)]}$$

where: $Z_{\alpha/2k}$ is the critical value of the standard normal distribution corresponding to an upper tail area $\alpha/2k$, α=0.05, k is the number of habitats used, and U_+ the number of used locations for that particular group. The selection coefficient w_i was significantly different from 1 where the confidence interval for w_i did not contain the value 1. If confidence intervals were over 1 then the category was selected and if under 1 then avoidance was inferred (Manly *et al.* 2002).

Selection ratios were compared using Bonferroni's inequality. The procedure is similar to means comparison in analyses of variance. The ratios were ranked from smallest to largest and compared two at a time using confidence intervals, where $Z_{\alpha/2k}$ was replaced with $Z_{\alpha/2l'}$, and l'=l(l-1)/2 is the total number of comparisons being made. Two selection ratios w_i and w_j, were declared significantly different if (w_i-w_j) did not contain zero (Manly *et al.* 2002). The α-level was set at p=0.05 for all comparisons between selection ratios.

4.2.8. Multivariate analyses

Resource selection functions (RSF) were constructed for multivariate analyses. The results of univariate analyses provided a rational for inclusion of predictors in the resource selection models. Two strategies were undertaken to (1) find the most parsimonious predictive model for each sex and season, and (2) assess the performance of *a priori* models (Table 4.2).

A Pearson's correlation matrix was examined using only continuous variables, with a. cut-off of 0.5 to assess correlation. Variables with correlation coefficients >0.5 were not included in the same model. A relative weight value was added to each point to control for differences in sample sizes. This equalised the influence of individuals and the used and available points on the model outcome. The weight attributed to each point was calculated as follows:

$$\textit{available weight} = \frac{\textit{used points}}{\textit{available points}}$$

$$\textit{individual weight} = \frac{\textit{used points for individual}}{\textit{(used points / number of individuals within group)}}$$

The RSFs were fitted using a binomial generalized linear model (GLM) derived by logistic regression (Boyce *et al.* 2002; Manly *et al.* 2002). The log-linear equation was assumed to characterise the influence of covariates on relative use:

$$w(x) = \exp(\beta_1 \cdot x_1 + \beta_2 \cdot x_2 + \beta_3 \cdot x_3 + ... + \beta_n \cdot x_n)$$

where β_i are selection coefficients for each covariate, xi, for i=1, 2, .., p (Johnson *et al.* 2006) and w(x) is a number proportional to the probability of use (Manly *et al.* 2002). Separate models were created for each season and sex at the home range and study area scales using the ecological variables as predictors of the binary dependent of a site being used (1) or randomly selected available sites (0). Models were estimated using logit-logistic regression in Systat 12 (San Jose, California, USA).

A priori models were constructed to investigate specific resource contexts (Table 4.2). Models were defined according to four contexts: (1) the 'food' model included variables that were associated with prey availability, without posing undue risk, by inclusion of cover variables to reduce exposure to predation; (2) the 'safe' model contained variables that provided the best hiding cover to reduce exposure to predation; (3) the 'risky' model contained open habitats with poor cover and higher predation risk and proximity to nomad camps as a measure of risks associated with humans; and (4) the temperature model included ravine habitats which provide cover from wind, solar radiation intensity and elevation.

Table 4.2: *A priori* candidate models for Pallas's cat habitat selection in the study area.

Model	Model Name	Model Structure (variables included)
1	food model	MS100 + Rav100 + dist S + Cover
2	safe model	Cover + slope + RH100 + Rav100
3	risky model	dist camp + risk + S100
4	temperature model	SRI + elevation + Rav50

4.2.9. Model selection

Akaike's Information Criterion (AIC) and log-likelihood values were used to assess model fit. All models with a ΔAIC<2 were considered to have empirical support based on the data (Burnham & Anderson 2002). The relative weight of evidence for each candidate model was assessed using Akaike's weights (AICw), providing a proportional weight where the sum of the competing models equals 1 (Burnham & Anderson 2002):

$$w_i(AIC) = \frac{\exp\left\{-\frac{1}{2}\Delta_i(AIC)\right\}}{\sum_{k=1}^{K}\left\{-\frac{1}{2}\Delta_k(AIC)\right\}}$$

Significant β coefficients within the model were those whose 95% confidence intervals did not include zero. Selection or avoidance was not inferred from covariates where the confidence intervals overlapped zero. Receiver operator characteristic (ROC) scores were included (i.e. area under ROC curve) for each selected model as an indicator of model performance. The ROC plot incorporates model sensitivity with specificity, where a perfect fit corresponds to 1 and a model with no predictive power has an area under the curve of 0.5.

4.3. Results

A total of 1439 non-denning radio-locations collected between May 2005 and November 2007 were used for modelling: male summer = 363 locations (9 cats), male winter = 236 locations (7 cats), female summer = 490 locations (13 cats) and female winter = 350 locations (10 cats).

4.3.1. Mortality

Mortality records were collected between January 2005 and December 2007. Of the 29 radio-collared Pallas's cats, 10 died; the cause of death was identified for 9 of these. A further 7 records were collected from un-collared Pallas's cats; 4 of these were from nomads' reports.

The timing of mortality was biased towards winter (Figure 4.1), with 82% of mortality records. This period coincided with poor vegetative cover, higher activity of males during the mating period, increased female activity from February to April and significantly more diurnal activity in comparison to the summer (Appendix 1). Mortalities caused by dogs and hunting were considered to be related to 'human' activity and accounted for 55% of the deaths of radio-collared cats.

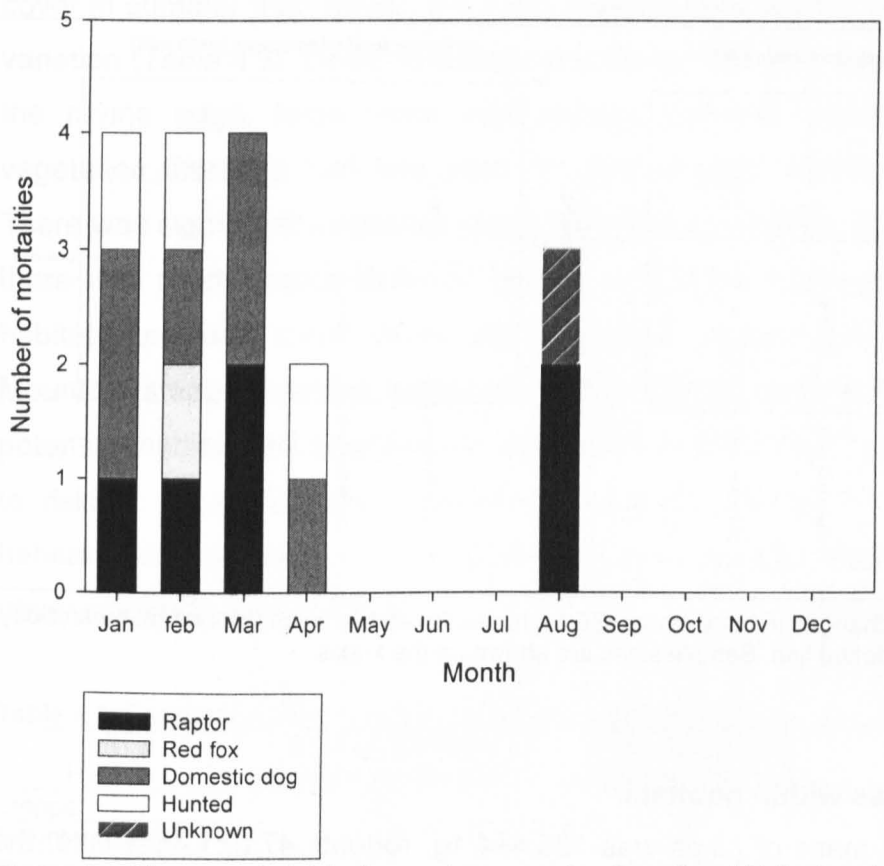

Figure 4.1: The annual distribution and causes of radio-collared Pallas's cat deaths and confirmed reports from herders.

4.3.2. Seasonal body mass

A total of 46 measurements of adult body mass were collected (27 males, 19 females). Male mass was lowest at the end of the mating season (March) and highest in autumn just before the mating season started (November: Figure 4.2). Average mass loss from highest to lowest over the year was 22% (maximum 32%). Most mass was lost in a short period of time during the mating season (December to March). Extreme cases were two males which lost 800g (19%) and

1050g (22%) in the space of 24 and 14 days respectively during the peak of the mating season. Both survived and gained mass during the summer.

Female body mass dipped in late summer (July to September) after raising kittens; mass was gained in autumn and lost again over the winter to reach a second low at the end of winter (February to March). The average loss in body mass from highest to lowest by females over the year was 23%.

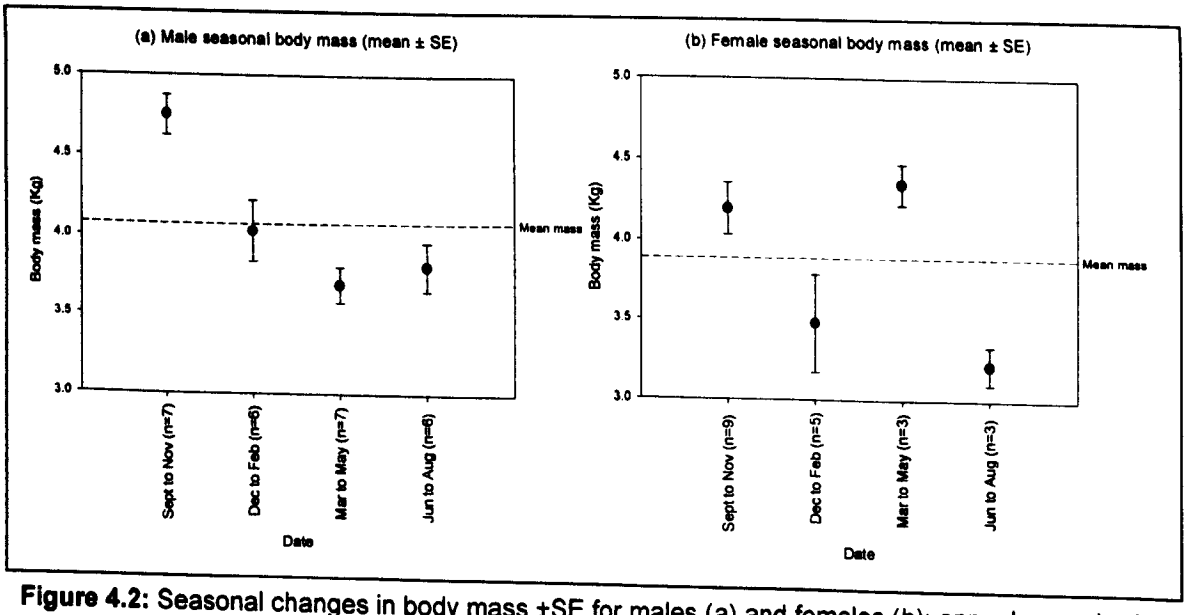

Figure 4.2: Seasonal changes in body mass ±SE for males (a) and females (b); annual mean body mass is shown with a dotted line. Sample sizes are shown on the x-axis.

4.3.3. Prey biomass within habitats

The average body mass of pikas was 135.4±4.1g, rodents 47.6±1.4g. Pikas, the preferred prey of Pallas's cats (Chapter 3), were very rare in rocky hillslopes, only occurring on the edge of this habitat. Total biomass was significantly lower in winter than summer ($F_{1,167}$=66.83, p<0.005). There were also significant differences between habitats in summer ($F_{1,81}$=5.48, p=0.005) but not winter ($F_{1,85}$=1.48, p=0.22). During summer, steppe had significantly greater biomass than mountain steppe (p=0.01) and rocky hillslope (p=0.01).

4.4.4. Detection distance and escape cover of habitats

As cover is an important factor affecting detection by predators, the safest habitats were those with the smallest detection distance. Additionally, as detection distance was a measure of disruptive cover or habitat complexity, habitats with smaller detection distances had better escape potential for Pallas's cats. Sighting distance was affected by seasonal changes in vegetative cover. There was a non-significant trend for steppe, and to a lesser extent mountain steppe, having more cover in summer than winter, but rocky hillslope and ravines showed no seasonal variation (Table 4.3). Cover in ravines and rocky hillslopes was mainly provided by the ravine edge, large rocks and uneven surfaces; seasonal differences in vegetation therefore had less effect on line of sight visibility in these habitats. There was significant variation in cover provided by habitats ($F_{3,76}$=44.1, p<0.005); there was no difference between ravines and rocky hillslopes (p=0.89) but both habitats provided more cover than mountain steppe and steppe (p<0.005). Mountain steppe provided better cover than steppe (p<0.005). Based on hiding potential, habitats were ranked for their safety and escape properties from safest to riskiest: rocky hillslope = ravine >> mountain steppe >> steppe, where (=) habitats have similar cover properties and (>>) habitats have significantly better cover properties (p<0.005).

Table 4.3: Seasonal change in sighting distances in each habitat.

Habitat	Average sighting distance (m) summer	Average sighting distance (m) winter	*t*	*df*	*p*
Steppe	66	114	1.94	20	0.07
Mountain steppe	35	48	1.67	18	0.11
Ravine	11	13	0.81	16	0.43
Rocky hillslope	13	15	0.34	18	0.73

4.4.5. Habitat selection patterns

Male summer: The best performing model at the study area scale was the same as for the home range scale (Tables 4.4 and 4.5). The most parsimonious model indicated the importance of rocky hillslope and mountain steppe habitats for foraging. Males minimised their distance to cover: cover was a highly significant predictor of presence. Surprisingly, significantly shorter distances to nomad camps than available were maintained. Selection ratios indicated stronger selection for the closest distance (<500m) to unoccupied nomad camps. Males were also found

significantly closer to nomad camps than females ($F_{1,851}$=8.02, p<0.005). The presence of vacant nomad camps was therefore a good predictor of male presence in the summer.

The 'risky' model was the highest ranked *a priori* model at both scales. All variables in the 'risky' model were highly significant, showing strong attraction to nomad camps, strong avoidance of steppe habitats and larger distances to risky habitats than expected. The second rank 'food' model was not comparable in parsimony (Table 4.6 and 4.7).

Male winter: There was a reduction in the magnitude of model β coefficients in winter, indicating less selection. The most parsimonious winter model was similar to the summer model, except the slope variable was dropped. Scale had an effect on model selection in winter, as closer proximity to nomadic camps was included in the best model at the study area scale, but was not part of the home range scale model. The exclusion of nomad camps from home range scale models indicated that nomad camps were not an important aspect of daily foraging decisions, which was expected since camps were occupied in the winter. Importantly, β coefficients indicated attraction at both scales, although the attraction was not significant at the home range scale. However, there was a significant increase in the distance to nomad camps in winter ($F_{1,597}$=84.21, p<0.005); males were also found closer to nomad camps than females ($F_{1,584}$=7.84, p=0.007).

The 'food' model was the highest ranked *a priori* model in winter at both scales, though a better model fit was apparent at the study area scale. The model achieved parsimony by its strong avoidance of steppe habitats, association with cover and selection of mountain steppe. Ravines were not selected and did not contribute to model fit.

Female summer: The most parsimonious model differed between the home range and study area scales. At the study area scale, there was strong selection for ravines, cover, high elevation, shorter distances to nomad camps and an

avoidance of steppe habitat. At the home range scale, rocky hillslope, ravine and cover variables were selected, while elevation and distance to nomad camp were dropped. The differences suggest that elevation and possibly nomad camps are cues for female cats when they are establishing their home range area but less influential during daily foraging. However, females were found closer to nomad camps in summer, when camps were unoccupied, than in winter when inhabited ($F_{1,838}$= 5.85, p=0.02), suggesting that humans had an effect on their selection patterns.

The *a priori* 'safe' model out-performed the 'food' model in summer at the home range scale, but model rank was reversed at the study area scale. This indicated that daily foraging patterns were governed by risk of predation; habitats with good prey abundance probably influenced the initial selection of home range areas.

Female winter: Weaker β coefficients indicated that habitat had less influence on the position of females in winter than in summer. Scale had no effect on the most parsimonious model: a high proportion of ravine, cover, higher elevations and greater distance to steppe were selected at both scales. Overall there was greater flexibility in the pattern of habitat selection in winter, with habitats that contained less cover but higher pika biomass used to a greater extent than in summer. While shorter distances to cover were selected, cover was significantly less influential than in summer. Cats were also found at significantly lower elevations in winter than in summer.

The best *a priori* model changed in comparison to summer at the home range scale, with the 'food' model outperforming the 'safe' model at both scales. The increased performance of the 'food' model was due to an increase in utilisation of mountain steppe habitats compared to summer.

Table 4.4: Top two habitat selection models for male and female Pallas's cats at the study area scale. β estimates are shown for model coefficients. A positive β indicates selection for MS, RH, Rav, elevation and slope; a negative β indicates selection where the resource was measured as a distance (cover, dist camp and dist S); * indicates significance α=0.05.

					β estimates +/-95 CIs							
	Study area models	ΔAIC	AICw	ROC	MS50	Rh150	Rav150	Cover	elevation	Slope	Dist camp	Dist S
M:sum	Rh150+US50+slope+cover+dist camp	0.00	0.71	0.86	0.924±0.343*	0.916±0.437*		-0.011±0.003*		0.021±0.016*	-0.060±0.010*	
	Rh150+US50+cover+ele+dist camp	2.61	0.29	0.85	1.133±0.351*	1.280±0.457*		-0.011±0.003*	-0.002±0.001*		-0.059±0.011*	
M:win	Rh150+US50+cover+dist camp	0.00	0.84	0.70	0.540±0.380*	0.812±0.483*		-0.004±0.002*			-0.013±0.010*	
	Rh150+US50+cover	5.06	0.16	0.70	0.550±0.380*	0.837±0.480*		-0.004±0.002*				
F:sum	Rav150+cover+ele+dist S+dist camp	0.00	>0.99	0.81			4.808±1.584*	-0.008±0.002*	0.004±0.002*		-0.012±0.008*	0.003±0.0007*
	Rh150+Rav150+cover+ele+dist camp	27.59	<0.01	0.80		1.228±0.385*	5.993±1.688*	-0.005±0.002*	0.004±0.001*		-0.013±0.008*	
F:win	Rav150+cover+ele+dist S	0.00	0.68	0.79			2.545±1.819*	-0.006±0.002*	0.005±0.002*			0.002±0.001*
	Rav150+cover+dist S	2.26	0.32	0.77			1.802±1.965*	-0.007±0.002*				0.003±0.001*

Table 4.5: Top two habitat selection models for male and female Pallas's cats at the home range scale. β estimates are shown for model coefficients. A positive β indicates selection for MS, RH, Rav, elevation and slope; a negative β indicates selection where the resource was measured as a distance (cover, dist camp and dist S); * indicates significance α=0.05.

					β estimates +/-95 CIs								
	Home range models	ΔAIC	AICw	ROC	MS50	Rh150	Rav150	S150	Cover	Elevation	Slope	Dist camp	Dist S
M:sum	Rh150+US50+cover+slope+dist camp	0.00	0.77	0.80	0.912±0.328*	1.481±0.413*			-0.010±0.003*		0.019±0.016*	-0.045±0.010*	
	Rh150+US50+ele+cover+dist camp	3.70	0.23	0.80	1.061±0.335*	1.740±0.430*			-0.010±0.003*	-0.001±0.002		-0.044±0.010*	
M:win	Rh150+US50+cover	0.00	0.78	0.67	0.812±0.393*	1.234±0.507*			-0.003±0.002*				
	S150+cover	3.79	0.22	0.67				-1.094±0.399*	-0.002±0.001*				
F:sum	Rh150+Rav150+cover	0.00	0.96	0.73		0.800±0.324*	4.330±1.542*		-0.006±0.002*				
	S150+Rav150+cover+slope	9.75	0.04	0.73			3.197±1.425*	-0.513±0.283*	-0.007±0.002*				
F:win	Rav150+cover+ele+dist S	0.00	0.78	0.69			3.952±1.762*		-0.005±0.002*	0.002±0.001*			0.002±0.001*
	Rav150+cover+dist S	2.53	0.22	0.68			3.733±1.755*		-0.006±0.002*				0.002±0.001*

Table 4.6: The rank of all *a priori* models for each sex, season and scale of analysis.

Extent ⟶	Study area				Home range			
Season	Male	Male	Female	Female	Male	Male	Female	Female
Model	summer	winter	summer	winter	summer	winter	summer	winter
Food model	2	1	1	1	2	1	2	1
Safe Model	3	2	2	2	3	3	1	2
Risky model	1	3	3	3	1	2	3	3
Temp model	4	4	4	4	4	4	4	4

Table 4.7: The top two ranked *a priori* models for each sex, season and scale of analysis.

Scale	Group	Model	Variables	ΔAIC	wi	ROC
Study area	M summer	Risky	S100+risk+dist camp	0.00	>0.99	0.84
		Food	dist steppe+cover+MS100+Rav100	115.92	<0.01	0.81
	M winter	Food	dist steppe+cover+MS100+Rav100	0.00	0.67	0.69
		Safe	cover+slope+Rh100+Rav100	2.07	0.33	0.69
	F summer	Food	dist steppe+cover+MS100+Rav100	0.00	>0.99	0.79
		Safe	cover+Slope+Rh100+Rav100	38.35	<0.01	0.78
	F winter	Food	dist steppe+cover+MS100+Rav100	0.00	>0.99	0.77
		Safe	cover+Slope+Rh100+Rav100	46.16	<0.01	0.75
Home range	M summer	Risky	S100+risk+dist camp	0.00	>0.99	0.79
		Food	dist steppe+cover+MS100+Rav100	68.09	<0.01	0.78
	M winter	Food	dist steppe+cover+MS100+Rav100	0.00	>0.99	0.68
		Risky	S100+risk+dist camp	11.06	<0.01	0.66
	F summer	Safe	cover+Slope+Rh100+Rav100	0.00	0.80	0.72
		Food	dist steppe+cover+MS100+Rav100	4.17	0.20	0.72
	F winter	Food	dist steppe+cover+MS100+Rav100	0.00	>0.99	0.68
		Safe	cover+Slope+Rh100+Rav100	25.59	<0.01	0.67

4.4. Discussion

The body mass of males was lowest after the mating season in March to April. Pallas's cats had very substantial fat reserves and adult males were able to lose up to 32% of their body mass over the mating season, survive and recover. Female body mass reached a low after raising young around July to August and again at the end of winter in February. The periods of low body mass experienced by both sexes indicated periods of decreased fitness and additional needs for food resources.

However, Pallas's cat's selection of food resources appeared restricted by predation by native carnivores and domestic dogs. Predation was the most common cause of mortality (N=17), accounting for 76% of deaths, plus an additional 18% that were hunted by local people. High levels of intra-guild

predation have been recorded in canids e.g. predation accounted for 78% of kit fox (*Vulpes macrotis*) mortality in California (Ralls & White 1995), 63% of swift fox (*Vulpes* velox) deaths in western Kansas (Sovada *et al.* 1998), 48% of swift fox deaths in Colorado (Kitchen *et al.* 1999) and 92% of gray fox (*Urocyon cinereoargenteus*) deaths in southern California (Farias *et al.* 2005). In comparison there are few records of felids being subject to intra-guild predation (Mills 1990; McOrist & Kitchener 1994; Laurenson 1995): this is the first study showing a notable intra-guild predation risk of a felid. The risk of predation was therefore expected to have an influence on Pallas's cat habitat choices, particularly since the available habitats provided different degrees of hiding cover and prey availability. Rocky hillslopes and ravines provided the best available disruptive cover, and were thus considered 'safe', whereas mountain steppe and steppe habitats provided significantly less cover and were classified as 'risky'. In terms of prey, rocky hillslopes had a negligible density of pikas, Pallas's cats preferred prey, whereas steppe had significantly higher pika densities. Weight loss, predation and the unequal costs and benefits associated with each habitat created situations where cats were expected to balance fitness benefits by changing their habitat selection patterns.

4.4.1. Do Pallas's cats select habitat?

Selection was demonstrated by the significantly higher probability of use of selected habitats against habitat availability. On average, Pallas's cats used a comparatively smaller niche (20-30%) than was available within their home range, with a strong focus on foraging areas within or near rocky hillslopes or in close proximity to habitats providing cover. As with their feeding preferences (Chapter 3), Pallas's cats' selection of habitat demonstrated a specialist pattern.

4.4.2. Do Pallas's cats select habitat to maximise prey or minimise risk?

Pallas's cats move slowly compared to other sympatric and predatory carnivores such as raptors, red fox and gray wolves. With few other options for escape, Pallas's cats appear to evade predation through behaviours that limit the ability of predators to capture cats and most probably through cryptic background matching. Thus Pallas's cats appear to be selecting 'safe' habitats which provide good disruptive cover and facilitate escape.

Pallas's cats consistently selected rocky hillslope, which had the lowest prey and pika density. In contrast steppe, which had the highest prey biomass, was avoided, suggesting that prey biomass was not a primary determinant of habitat selection. Mountain steppe was selected strongly in some seasons, but had better cover than steppe and may have been favoured because it was adjacent to rocky hillslope. Mountain steppe was suitable pika habitat and it is likely that mountain steppe was an important feeding habitat.

Males and females had similar selection patterns but exhibited subtle differences which could be related to their specific life histories. Males used open habitats more than females, suggesting less sensitivity towards risk. This may arise from the need to access prey and achieve high body reserves to reproduce successfully and survive the associated large weight loss. Conversely, females appeared to place a greater emphasis on safety, particularly in summer when caring for young. During this time *a priori* models indicated that, at the home range scale, safety explained more variation in habitat use than food. Investment protection while with young may be an important factor, as death of the mother would also result in death of the kittens (Clark 1994).

For many species, foraging costs are dominated by the cost of predation. For instance, wild dogs (*Lycaon pictus*) are found at low densities in areas with high food availability but high predator density (Mills & Gorman 1997). Similarly, the distribution of foraging bottlenose dolphins (*Tursiops aduncus*) reflects trade-offs between predation risk and food availability (Heithaus & Dill 2002). Predation risk can therefore have a dramatic effect on the behaviour of many carnivores that must balance their foraging decisions according to food and risk (Brown 2000; Brown & Kotler 2004). The high selection of Pallas's cats for rocky hillslope and ravines, habitats with reduced predation risk but lower prey densities, suggested that the risk of predation dominated the selection behaviour of Pallas's cats. The 'safe' niche comprised such a small proportion of the landscape and was selected to such an extent that Pallas's cats could be labelled 'safety specialists'. According to theory, 'specialization increases with a decrease in the cost of search' (Futuyma

& Moreno 1988). Pallas's cats' appear to have decreased their search costs and increased fitness by specialising on habitats that minimise their risk of predation.

4.4.3. Does low prey biomass result in trade-offs between safety and risk?

There was a large seasonal variation in food abundance in the study area, and so winter provided a natural experiment to test whether Pallas's cats trade off food and safety. In summer, when prey was relatively abundant, males used relatively safe rocky hillslopes and adjacent mountain steppe habitat as core habitat, even though these habitats had lower prey availability. In winter, males significantly decreased their use of rocky hillslopes, selecting areas of steppe with higher prey biomass. The habitat switching effectively increased access to prey, and indicated a food-safety trade-off. However, as males seek breeding opportunities with multiple females in winter, the increased use of steppe may result from a need to traverse steppe to gain access to females. The increased risk, associated with use of steppe habitat, would therefore result in a payoff of increased reproductive potential. Separating the food and reproductive benefits are difficult, but the large loss of body mass over the winter indicates an emphasis on reproduction over food acquisition.

Females also selected less productive, 'safe' habitats in summer. In winter they increased their use of riskier habitats, essentially trading good cover and safety for higher food availability. Perhaps the impending costs of maternal care, starting in April, and their relatively low winter body mass made the increased risks worthwhile. The need of females to gain body reserves was also supported by their greater activity during the pre-maternal period than at other times of the year (Appendix 1).

The changes in the environmental conditions experienced by Pallas's cats, in terms of prey availability, mating opportunities and predation risk, altered the terms of the trade-off between risks and benefits, modifying the behavioural optimum (Clark 1994). While safety was emphasised in habitat selection throughout the year, being safe is of little use until sufficient energy reserves are gained that increase survival or the likelihood of reproduction. As a result, Pallas's cats traded the use of safe habitats when fitness benefits required that additional risks were

taken, which was confirmed by substantially more mortalities taking place in winter than summer. Differences in habitat use among seasons were therefore due to trade-offs between fitness benefits and safety. Unlike previous studies that have noted animals adaptively modifying habitat use patterns to counteract increases in predation risk (Heithaus & Dill 2002), Pallas's cats increased use of open habitats in winter even though the low vegetative cover means that the risk is greatest. This emphasises the importance of adaptive habitat switching to Pallas's cats to increase energy reserves or reproductive opportunities.

4.4.4. Do Pallas's cats avoid areas with human disturbances?

Pallas's cats, particularly males, were attracted or indifferent to the presence of nomad camps. Males showed significant selection for habitats surrounding nomad camps at all times except winter at the home range scale. Females appeared more sensitive to the camps, showing non-significant aversion to camps in the winter. The patterns therefore showed a weak effect of camp occupation in winter, but importantly camp occupation did not elicit significant avoidance behaviour. The lack of avoidance may be maladaptive for three reasons: (1) increased encounters with humans is likely to increase Pallas's cat mortality; for example, two radio-collared Pallas's cats were shot during the study and one was caught in a leg-hold trap; (2) nomadic camps keep 2-3 domestic dogs, which kill Pallas's cats, and so predation risk should increase closer to nomad camps; and (3) nomad camps harbour a risk of disease, because cats near camps are more likely to come into contact with zoonotic diseases from domestic hosts (Gog *et al.* 2002). A serosurvey of the study population showed Pallas's cats had been exposed to feline immunodeficiency virus, haemoplasma, canine distemper virus, canine parvovirus and a low level of toxoplasmosis (Brown *et al.* submitted; M. Brown pers. comm.). All of these diseases have potential domestic reservoirs. Mortality of Pallas's cats due to toxoplasmosis has been verified (Brown *et al.* 2005), and the consequences of other diseases are potentially severe (e.g. Daszak *et al.* 2000; Ikeda *et al.* 2000; O'Brien *et al.* 2006; Willi *et al.* 2007).

Although data were not available to explain the strong attraction of Pallas's cats to nomad camps in summer, there are two possibilities: (1) wolves and red foxes are actively hunted by Mongolians which may result in a lower density of these

species around camps; Pallas's cats could be attracted to the predator-free space; or (2) alternatively, greater prey biomass around camps may attract Pallas's cats as over-winter disturbances, seed inputs and fertilisation by livestock may promote vegetation growth during the summer fallow season (Bulow-Olsen 1980; Hobbs & Huenneke 1992). The changes in vegetation are likely to favour higher pika density, and gerbil density may increase as the granivores take advantage of over-winter seed deposits in livestock faeces (Zhong *et al.* 1999; Komonen *et al.* 2003).

4.5. Conclusions

The observed selection patterns suggest that Pallas's cats are habitat specialists, selecting habitats that provide superior cover from predators but have lower densities of their preferred prey, suggesting that predation risk is the principal determinant of fitness. Although safety from intra-guild predation was always an important factor, trade-offs occurred throughout the year according to the fitness benefits obtainable by altering habitat selection.

The high percentage of human caused mortality may represent a limitation on population survival. Because Pallas's cats occur at low densities, high mortality would have a relatively higher impact on population vulnerability. The lack of avoidance of nomad camps may aggravate this situation by increasing Pallas's cats' exposure to human or domestic dog encounters. Future conservation actions should take into account the potential cumulative effects of disturbances on mortality rate (Johnson *et al.* 2005) in light of changes in density and lifestyles of the nomadic peoples of the steppe ecosystem.

Chapter 5

Factors associated with critical denning habitat of Pallas's cat

Summary

1. Dens provide many animals with important shelter and can be a population limiting resource.
2. I measured Pallas's cat den habitat selection using resource selection models. *A priori* models of den use were constructed and an information theoretic approach used to assess model rank.
3. Pallas's cats used rock crevices and marmot burrows on a daily basis, for giving birth and raising young, thermoregulation, feeding and even mating. Pallas's cats were out of reach of predators within dens, which had a critical predator avoidance function.
4. The 'den habitat' model was the most parsimonious in 5/6 cases, indicating that the habitat of the immediate surroundings of the den were most important.
5. Males and females selected slightly different denning habitats. Females favoured habitats providing good cover from predators, particularly when raising young. Males appeared to select habitats with good access to prey resources and possibly females.
6. Given the frequency of den use, dens are an important component of Pallas's cat habitat and it is unlikely they could exist in areas without such resources.

5.1. Introduction

Various factors can influence habitat use, but the general assumption is that individuals select habitats where their fitness is maximized in accordance to the activity they need to perform (Szor *et al.* 2008). Habitat must therefore provide the four main environmental components: food, water, cover, and denning sites (Litvaitis *et al.* 1996).

Den location is often related to factors such as the ease of escape from predators (Ruggiero *et al.* 1998) or the proximity of available food resources (Pruss 1999; Arjo *et al.* 2003; Szor *et al.* 2008). Suitable dens are often critical population limiting resources, particularly for animals which cannot excavate their own shelters (Fernandez & Palomares 2001; Zeilinski *et al.* 2004). For example, the availability of rock piles was a significant factor explaining mammal extinctions in Australian islands because they provided refugia from exotic predators (Burbidge & Manly 2002).

Studies of den sites have mostly concentrated on their microhabitat attributes, such as construction materials (Fernandez & Palomeres 2001), topography (Seroyodkin *et al.* 2003) or depth, entrance diameter and number (Zhang *et al.* 2006). These fine scale and structural attributes can be used to conserve or restore dens if they are a limiting resource (Zhang *et al.* 2006). However, relatively few studies have evaluated den habitat selection relative to availability, which is necessary to demonstrate selection (Zielinski *et al.* 2004; Reynolds-Hogland *et al.* 2007). Selection in turn distinguishes key factors influencing the use of dens, shedding light on a species' ecology, physiology and the constraints to which it is exposed (Szor *et al.* 2008).

Pallas's cats primarily depend on rock and earth dens dug by other mammals such as marmots (*Marmota sibirica*); dens are used on a daily basis throughout the year. Pallas's cats give birth and rear young within dens and, since they are predated by a number of large aerial and terrestrial predators, dens are likely to be used for predator avoidance. Dens are also likely to have a thermoregulatory role during the cold winter. However, in the absence of any quantified data on den use, my first objective was to determine whether Pallas's cats were selecting specific habitats for denning by testing den use against availability. The selection patterns were interpreted using data on behaviour, habitat-specific prey biomass and the cover properties of available habitats. Differences between den selection due to season and sex were also assessed. Seasonal trade-offs between habitats were expected because of the dramatic changes in habitat characteristics resulting from vegetative dieback and seasonal changes in prey biomass. Thus den selection by

Pallas's cats was expected to reflect the need to balance predation risk and feeding opportunities, since selection favours individuals that optimally balance the benefits of risk reduction against costs (Lima 1998). Differences between sexes were expected because of their different life histories. Females generally prioritise giving birth and raising kittens, whilst males strategically maximise their reproductive opportunities (Sandell 1989). Previous studies have shown that females are extremely selective, particularly when choosing their maternal den (Ruggiero *et al.*1998; Fernandez & Palomares 2001); males are comparably less selective (Zielinski *et al.* 2004). Season was also predicted to be influential in den selection because of the large range in temperature experienced in the study area and because temperature stability within dens is advantageous for thermoregulation, particularly in sheltering animals from the extreme cold of winter (Buskirk 1984; Davenport 1992). I aimed to answer the following three questions:

1. Do Pallas's cats select dens based on the habitat attributes of the dens?
2. Is den habitat selection is related to trade-offs between safety and efficiency in gaining food?
3. Are selection patterns are specific to seasons and sexes?

5.2. Methods

5.2.1. Radio-tracking and observations

Radio-collared Pallas's cats were re-located every 1-5 days. When an inactive signal was heard from all three triangulation points, the signal was followed to identify the den site and record its GPS coordinates. All Pallas's cat dens were separated into male and female groups and those used in the summer, winter and maternal dens used by females while raising kittens.

Occasionally, the cat was found stationary above-ground: it was then approached at walking pace and its escape behaviour recorded. These were classified as: (1) entered nearest bolt-hole; (2) ran to nearest cover to escape; or (3) assumed itself camouflage and remained motionless. Denning behaviour was also recorded opportunistically, through observing feeding remains, sign and other behaviours.

5.2.2. Den site distribution and availability

Den sites used by Pallas's cats included marmot burrows and rocky fissures. The habitat specific abundance of dens were surveyed by walking transects. Transects were selected using a stratified random technique where the study area was split into 5 equal-sized regions and random points were generated within the regions or, in the case of ravine transects, random points were generated within ravines. Non-ravine transects were paired to a randomly-generated bearing indicating the transect direction. Transects were then conducted sequentially where the random point indicated the transect start and the bearing the direction to be walked.

Two methods were used to survey den sites. Distance sampling was used to estimate den site density in rocky hillslopes, mountain steppe and steppe, (Buckland *et al.* 2001). In ravines, only the distance to the ravine edge could be observed, so total counts of dens were taken and the density calculated by multiplying the ravine width by the transect length.

A chi-square test was used to compare den use against den availability. Expected use patterns were calculated by measuring the percentage of habitats available within the combined home ranges of radio-collared Pallas's cats' and the number of dens per km^2 within each habitat by using the formula:

$$\exp i = (Di \times Ai) / \sum Di$$

where: exp*i* =the expected proportion of dens within habitat *i*, D*i* =dens per km^2 in habitat *i* and A*i* =available proportion of habitat *i*.

5.2.3. Model construction

A used (den fixes) and available (randomly generated points) design was used to construct univariate resource selection ratios and multivariate resource selection functions (Manly *et al. 2002*). Only dens that had confirmed use on more than one occasion were included in the analyses, thus excluding potential bolt-holes used for short-term cover. Used den sites were entered into a GIS database and complimentary random available locations were generated using Hawth's analyses tools (Beyer 2004) for ArcGIS 9.2. Two orders of magnitude greater random

available points were generated than those used so that used sites were an acceptably small proportion of those available (Johnson *et al.* 2006).

Because only 1-2 den sites were identified for each Pallas's cat, there was little individual variation in the sample and so I used a special case of 'design 1' studies (Manly *et al.* 2002; Ciarniello *et al.* 2005). Since animals selected dens from within their home ranges, available locations were only drawn from within the combined seasonal home ranges of male and female study animals.

Habitat covariates were measured for the used and available samples within a GIS database (Table 5.1). The effect of scale on selection patterns was investigated by measuring the habitat proportions available in concentric circles 50 and 600m surrounding dens, thereby varying the grain size. A correlation matrix of all model variables was examined prior to model construction and variables with correlations >0.5 were not included in the same model to prevent spurious results.

Table 5.1: The variables measured at each den site.

Variable	Type	Description
Dist S	Continuous	Distance (m) to steppe habitat
Dist MS	Continuous	Distance (m) to mountain steppe habitat
Dist RH	Continuous	Distance (m) to rocky hillslope habitat
Dist Rav	Continuous	Distance (m) to the ravine habitat
Habitat	Categorical	Habitat type at the den site (rocky hillslope, mountain steppe, steppe or ravine)
S50 & 600	Continuous	The proportion of steppe habitat within 50 and 600m circles surrounding the identified point
MS50 & 600	Continuous	The proportion of mountain steppe habitat within 50 and 600m circles surrounding the identified point
RH50 & 600	Continuous	The proportion of rocky hillslope habitat within 50 and 600m circles surrounding the identified point
RAV50 & 600	Continuous	The proportion of ravine habitat within 50 and 600m circles surrounding the identified point
Slope	Continuous	The slope (°) at the identified point
Elevation	Continuous	Elevation (m) at the identified point
Solar radiation Index	Continuous	Index of solar intensity (Keating *et al.* 2007)

5.2.4. Univariate analyses

Resource selection ratios were constructed for each variable to identify the most important predictors of Pallas's cat den sites and to aid interpretation of selection

patterns. All variables were first converted into categorical variables. Selection ratios with Bonferroni corrections for multiple comparisons were then constructed as outlined in Chapter 4.

5.2.5. Multivariate analyses

The univariate analyses guided modelling by indicating the relationships between individual variables and selection. Resource selection functions (RSF) were constructed for multivariate analyses, using a binomial generalized linear model (GLM) derived by logistic regression (Boyce 2002). The influence of covariates on relative use was characterised by the equation:

$$w(x) = exp(\beta_1 \cdot x_1 + \beta_2 \cdot x_2 + \beta_3 \cdot x_3 + ... + \beta_n \cdot x_n)$$

where β_i are selection coefficients for each covariate, *xi*, for $i = 1, 2, \ldots, p$ using the measured ecological variables as predictors of the binary dependent of used (1) or randomly selected sites (0); w(x) is a number proportional to the probability of use (Manly *et al.* 2002). All variables except den habitat were continuous data. For analyses of den habitat, mountain steppe was assigned as the dummy variable and selection was measured relative to this habitat. Models were estimated using logit-logistic regression modelling in Systat 12 (San Jose, California, USA).

A priori candidate models were constructed according to biologically relevant contexts. Only non-correlated variables were used in the same model (Table 5.2). The following models were constructed: (1) the 'den habitat' model used only categorical data (Habitat) describing the habitat type in which the den was located. Den habitat therefore assessed the importance of the immediate, microhabitat selection of the den; (2) the 'safety' model included the proportion of rocky hillslope and ravine habitats, which provide good cover, within 50m of the den (RH50 and Rav50) and the slope (Slope) of the den, where steeper slopes were assumed to provide better cover by reducing the sighting angle; (3) the 'food' model incorporated the proportion of mountain steppe and ravine with 50m of the den (MS50 and Rav50) and the distance to the edge of steppe habitat, since these

habitats are associated with high prey availability; (4) the 'temperature' model included ravines within 50m (Rav50), since these provide cover from wind, solar radiation intensity (SRI) and elevation at the den (Elevation), all of which were associated with exposure to weather; (5) the 'small scale' model included the proportions of habitats within 50m of the den (RH50, Rav50 and MS50); and (6) the 'large scale' model included habitat proportion within 600m of the den (RH600, Rav600 and MS600). By comparing the small and large scale models the relative importance of habitats close and far from the den was measured and the scale of den selection assessed.

Table 5.2: *A priori* candidate models for Pallas's cat den site selection.

Model	Model	Model structure (variables included)
1	Den habitat	Habitat
2	Safety	RH50 + Rav50 + Slope
3	Food	Rav50 + MS50 + dist S
4	Temperature	SRI + Elevation + Rav50
5	Small scale	RH50 + Rav50 + MS50
6	Large scale	RH600 + Rav600 + MS600

5.2.5. Model selection

Model selection and ranking was based on Akaike's Information Criterion for small sample sizes (AICc). The model with the lowest AICc score represented the most parsimonious model. The relative weight of evidence for each candidate model was assessed using Akaike's weights (AICw), providing a proportional weight where the sum of the competing models equals 1 (Burnham & Anderson 2002).

All models within 2 AIC of the most parsimonious model were considered to have empirical support based on the data (Burnham & Anderson 2002). Significant β coefficients (ln odds ratio) within the RSF model were those whose 95% confidence intervals did not include zero. Selection or avoidance was not inferred from covariates where the confidence intervals overlapped zero. Receiver operator characteristic (ROC) scores were included (i.e. area under the ROC curve) for each selected model as a further indicator of model performance.

5.3. Results

A total of 98 dens used by 19 different radio-collared Pallas's cats were identified (Figure 1). These included 17 maternal dens, 18 female summer dens, 26 female winter dens, 24 male summer dens and 13 male winter dens. Residency times for summer, winter and maternal dens are shown in Table 5.3. The short residency times reflect the shifting pattern of range-use and their need to find alternate shelters.

Table 5.3: Number of dens identified as used by Pallas's cats, and mean residency times in individual dens during summer, winter and maternal periods.

Sex	Dens used (mean, range, *n*)	Time at winter den (mean, range, n)	Time at summer den (mean, range, *n*)	Time at maternal den (mean, range, *n*)
Male	6.5 (5-9) *7*	3 (2-9) *6*	9 (2-28) *16*	
Female	12.5 (7-21) *11*	6 (3-15) *21*	3 (2-5) *5*	25 (4-70) *20*

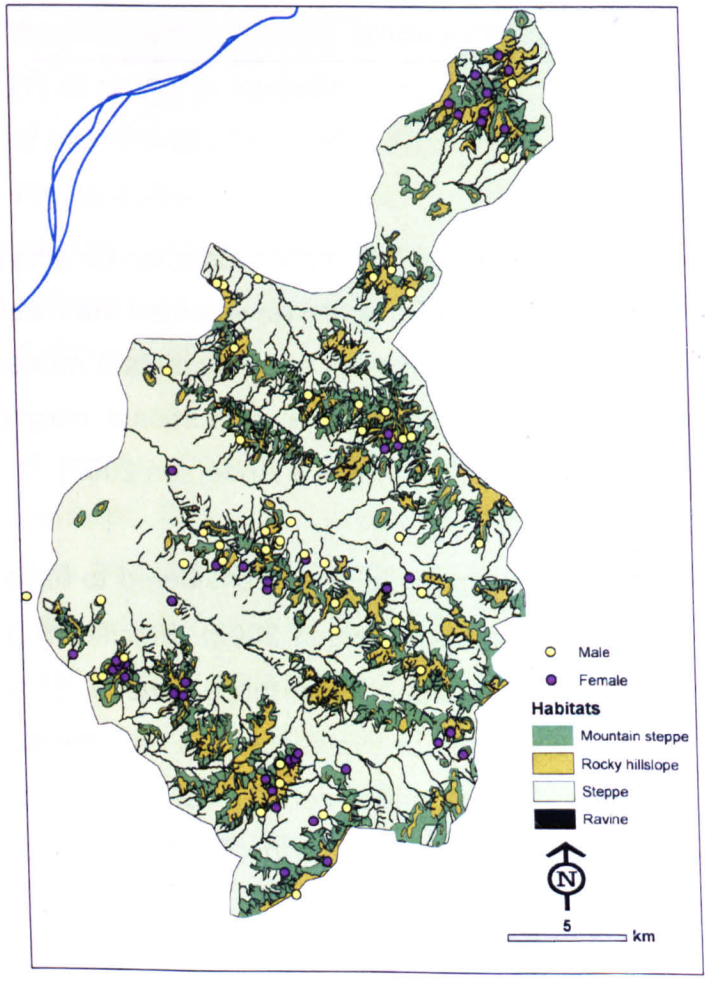

Figure 5.1: Positions of male and female dens in relation to habitats.

5.3.1. Behavioural observations relating to dens

In order of importance, dens were (1) Siberian marmot burrows, (2) rock piles, (3) rock cliffs and (4) rock burrows constructed by *Alticola semicanus* colonies. Den preferences changed throughout the year (Table 5.4). Marmot burrows were of two types: shallow summer holes (~1m depth by 4-6m long) and deeper winter hibernicula (1.5-2m depth by 5-10m long).

Table 5.4: Percentage of dens within rock spaces (mostly natural) and marmot burrows. Sexes were combined, showing samples sizes in brackets.

Den type	Maternal dens (17)	Summer dens (42)	Winter dens (39)	Total
Rock dens	68%	30%	3%	34%
Marmot burrow	32%	70%	97%	66%

Pallas's cats would also seek out bolt-holes when danger threatened. This was simulated by approaching a foraging cat and watching its reaction: on 43% of occasions (n=30) the cat ran to the nearest bolt-hole (marmot burrow or crevice), on 30% of approches it slunk down and froze next to rocks or vegetation assuming itself hidden and on 27% of approaches it moved into cover such as rocky areas or ravines and ran. However, when pursued and given the option, cats always sought a bolt-hole or their own den.

On two occasions, Pallas's cats were observed to take prey to a den and consume it with their hindquarters within the den and forequarters at the entrance: I also found 26 small mammal visera, 5 uneaten small mammals and 10 remains of birds outside used den sites, indicating food was sometimes taken back to dens and consumed.

On two occasions during the mating season (10th and 17th of Feburary) radio-collared male and female Pallas's cats were found within the same den. The types and duration of sounds heard from within the den indicated copulation: both pairs were together or in close vicinity of each other for 3-4 days.

5.3.2. Resource selection analyses

Males: During the summer the 'den habitat' model was the most parsimonious. The 'small scale' habitat and 'safety' models were ranked second and third, but were not comparable in AIC to the 'den habitat' model. Males selected mountain steppes for den use, significantly avoided steppe and showed a non-significant avoidance of rocky hillslopes. Rocky hillslopes were selected within 50m of the den and mountain steppe was selected within 50 and 600m of dens. Although non-significant, elevation had a negative β coefficient, indicating a preference for lower elevations. Overall, the habitat the den was in was important but, unlike females, males selected dens within mountain steppe. Mountain steppe was also highly selected in the den surroundings at small and large scales.

During winter, the 'den habitat' model performed the best, but the difference was not as clear as in summer. The 'small scale' and 'food' models were next in rank. In winter, dens within ravines were significantly selected in preference to those in mountain steppe; steppe was again avoided as a den habitat. There was also selection for mountain steppe and ravines within 50m of the den. Negative β coefficients indicated a non-significant preference for lower elevations, shallower slopes and closer distances to steppe habitat. This was the opposite of female winter preferences. Overall, dens within ravines were selected and mountain steppe and ravine habitats were selected in the den surroundings. Males in winter were the only group to show an attraction to dens closer rather than far from steppe habitat.

Female maternal dens (April to July): The 'den site habitat' model was the most parsimonious for maternal females. All other models were >2.0 AIC of the best model, indicating they were not comparable. The second and third ranked models were 'small scale' and 'safety', followed by the 'large scale', 'food' and then 'temperature' models, which performed poorly. Significant selection was shown for dens within rocky hillslope and ravine habitats; steppe was avoided but not significantly relative to mountain steppe. Rocky hillslope and ravine habitats were also selected within 50m of the den, emphasising the importance of the immediate surroundings of the den. Rocky hillslopes continued to be selected at 600m, though this could have been a residual from the strong selection for rocky

hillslopes at the small scale. Steppe was strongly avoided at all scales. Females selected higher elevations than those available within the home range. Overall, strong selection was shown for rocky hillslopes and ravines for maternal dens; selection was strongest at the smallest scales but continued to large scales. Dens were located at the highest elevations and at greatest distances from steppe habitat.

Non-maternal female dens: Summer den selection was similar to the maternal period. The 'den habitat' model was the most parsimonious model; the 'food', 'temperature' and 'large scale' models were next in rank and similar to each other, but not within 2 AICc of the most parsimonious model. The 'safety' and 'small scale habitat' models performed least well.

Dens were chosen significantly more often in rocky hillslopes and ravines than mountain steppe. Rocky hillslope was selected in the area 50 and 600m from the den site but more clearly at the larger scale. Steeper slopes were used and there was a trend to use higher elevations. There was also selection of dens with lower solar radiation indexes, or shady aspects. Overall, there was strong selection for dens within rocky hillslopes and ravines. The main difference between summer and maternal dens was the higher rank of the 'food' and 'temperature' models, indicating a change in importance of environmental factors when not raising young. There was also a shift in the importance of scale, as habitats further from the den became more important.

Selection patterns changed during winter. The 'den habitat' model performed least well and the 'small scale' model was the most parsimonious. No other models were within 2 AIC of the 'small scale' model. Strong selection was shown for rocky hillslopes, ravines and mountain steppe within 50m. Rocky hillslopes and mountain steppe were also significantly selected within 600m of the den. Similar to previous seasons, steppe was significantly avoided. Overall there was a change in selection, as the habitat which the den was located was substantially less important. The influence of slope and elevation on selection was also reduced, indicating more use of lower elevations. The habitats in the surroundings

increased in importance in winter and mountain steppe was selected more than in other seasons.

Table 5.5: Candidate model rank indicating the relative probability of male Pallas's cat den site locations in (a) winter and (b) summer. Models are ranked according to AICc scores; ΔAICc indicates the difference between the best and lower ranked models, AICw the proportional weight of evidence for each model and ROC model performance.

(b) Male summer

Model rank	Variables	β	ΔAICc	AICw	ROC
Den site	Habitat		0.00	1.00	0.75
Habitat	RH	-0.644			
	Rav	0.272			
	S	-2.187*			
Small	RH50	1.493*	+12.32	0.00	0.66
Scale	Rav50	1.874			
Habitat	MS50	1.377*			
Safety	RH50	0.769*	+14.75	0.00	0.67
	Rav50	1.710			
	Slope	0.060			
Food	Rav50	1.208	+16.38	0.00	0.67
	MS50	0.967*			
	Dist S	0.002			
Large	RH600	0.640	+16.77	0.00	0.65
Scale	Rav600	-12.147			
Habitat	MS600	2.765*			
Temperature	SRI	-0.415	+17.02	0.00	0.62
	Elevation	-0.004			
	Rav50	1.738			

(a) Male winter

Model rank	Variables	β	ΔAICc	AICw	ROC
Den site	Habitat		0.00	0.61	0.74
Habitat	RH	0.742			
	Rav	1.435*			
	S	-1.088			
Small	RH50	1.006	+2.64	0.16	0.73
Scale	Rav50	4.627*			
Habitat	MS50	1.462*			
Food	Rav50	4.467*	+3.37	0.11	0.72
	MS50	1.386*			
	Dist S	-0.001			
Temperature	SRI	-0.397	+4.90	0.05	0.70
	Elevation	-0.003			
	Rav50	4.843*			
Safety	RH50	0.705	+5.71	0.04	0.71
	Rav50	4.450*			
	Slope	-0.014			
Large	RH600	3.234*	+7.01	0.02	0.66
Scale	Rav600	-2.116			
Habitat	MS600	-1.287			

Table 5.6: Candidate model rank indicating the relative probability of female Pallas's cat maternal den site locations. Models are ranked according to AICc scores; ΔAICc indicates the difference between the best and lower ranked models, AICw the proportional weight of evidence for each model and ROC model performance.

Female maternal					
Model rank	Variables	β	ΔAICc	AICw	ROC
Den site	Habitat		0.00	1.00	0.86
Habitat	RH	2.246*			
	Rav	2.064*			
	S	-1.781			
Small	RH50	3.092*	+12.94	0.00	0.83
Scale	Rav50	5.908*			
Habitat	MS50	1.121			
Safety	RH50	2.691*	+14.26	0.00	0.83
	Rav50	5.743*			
	Slope	0.011			
Large	RH600	5.219*	+19.57	0.00	0.78
Scale	Rav600	-17.246			
Habitat	MS600	2.420			
Food	Rav50	3.486*	+25.51	0.00	0.80
	MS50	-0.237			
	Slope	0.004*			
Temperature	SRI	-0.351	+25.76	0.00	0.71
	Elevation	0.007*			
	Rav50	3.908*			

Table 5.7: Candidate model rank indicating the relative probability of female Pallas's cat den site locations in (a) summer and (b) winter. Models are ranked according to AICc scores; ΔAICc indicates the difference between the best and lower ranked models, AICw the proportional weight of evidence for each model and ROC model performance.

(a) Female summer					
Model rank	Variables	β	ΔAICc	AICw	ROC
Den site	Habitat		0.00	0.95	0.76
Habitat	RH	1.995*			
	Rav	2.064*			
	S	-0.395			
Food	Rav50	2.109	+7.51	0.02	0.75
	MS50	0.361			
	Dist S	0.005*			
Temperature	SRI	-1.255*	+8.15	0.16	0.74
	Elevation	0.005			
	Rav50	0.764			
Large	RH600	4.049*	+9.70	0.01	0.68
Scale	Rav600	-0.035			
Habitat	MS600	-0.829			
Safety	RH50	0.640	+10.90	0.00	0.73
	Rav50	3.163			
	Slope	0.092*			
Small	RH50	1.532*	+13.44	0.00	0.68
Scale	Rav50	2.999			
Habitat	MS50	1.103			

(b) Female winter					
Model rank	Variables	β	ΔAICc	AICw	ROC
Small	RH50	3.177*	0.00	0.99	0.82
Scale	Rav50	6.278*			
Habitat	MS50	2.340*			
Safety	RH50	2.139*	+10.07	0.01	0.77
	Rav50	5.481*			
	Slope	0.020			
Food	Rav50	4.282*	+15.93	0.00	0.78
	MS50	0.935			
	Dist S	0.004*			
Large	RH600	3.361*	+17.99	0.00	0.73
Scale	Rav600	-1.453			
Habitat	MS600	3.046*			
Temperature	SRI	-0.708	+18.93	0.00	0.71
	Elevation	0.004			
	Rav50	4.687*			
Den site	Habitat		+30.69	0.00	0.57
Habitat	RH	0.491			
	Rav	0.742			
	S	-1.899*			

5.3.2. Distribution and availability of potential den Sites

A total of 53km of transects were walked to locate potential den sites (Table 5.8). Dens were most numerous in mountain steppe, closely followed by ravines. There were far fewer dens in steppe and dens were uncommon in rocky hillslopes (Table 5.9). According to χ^2-tests, dens within rocky hillslopes were used significantly more than expected (χ^2=175.0, *df*=4, p<0.001), as were dens within ravines (χ^2=13.5, *df*=4, p=0.009). However, as more than 10% of expected frequencies of rocky hillslope and ravine were less than 5, the test should be interpreted with caution (Quinn & Keogh 2002). Dens within mountain steppe were used less than expected (χ^2=14.9, *df*=4, p=0.005). There was also a non-significant trend for steppe to be used less than expected for denning (p= 0.06).

Table 5.8: Transect length and number used to locate potential den sites.

Habitat	Ravine	Steppe	Mountain steppe	Rocky hillslope
Total length of transects	4327 m	28,372 m	13,112 m	7101 m
Number of transects	4	11	10	8

Table 5.9: The density of potential den sites in different habitats, coefficient of variation and 95% confidence intervals.

Habitat	Density (dens/ km^2)	%CV	95% CI of density	
			Lower	Upper
Steppe	470	33	207	1064
Mountain steppe	2319	9.17	1925	2794
Rocky hillslope	355	30.8	172	731
Ravine	1508			

5.4. Discussion

My results addressed factors affecting microhabitat selection by Pallas's cats after they have chosen a suitable home range area. All of the den models significantly explained the selection of den habitat, but the performance of different models and variables varied according to season and sex. Dens provided Pallas's cats with cover for resting, thermoregulation, mating, feeding, giving birth, raising kittens and cover from predators. While it is likely that structural factors influence the use of individual dens, dens within rocky hillslopes and ravines were used disproportionately to availability, thus supporting the hypothesis that dens were selected according to habitats surrounding the dens.

5.4.1. Is den selection is related to trade-offs between risk and food?

Experimental studies have shown that, when given a choice, animals prefer circumstances or habitats in which predation risk is low, even if foraging opportunities are reduced (Power 1984; Lima *et al.* 1985). While the role of dens in reducing predation risk is relatively unexplored (Caro 2005), the habitats surrounding the dens are known to affect the risk of predation (Ylonen *et al.* 2003). Pallas's cats are at high risk of predation (Chapter 4), and avoiding predation was likely to be a particular issue when exiting the den, before the surroundings have been assessed for predation risk, and when entering the den while not alerting predators of their location. Thus den sites should be chosen to ensure maximum safety, while the areas surrounding the den should balance the need for prey and risk of predation.

Risk aversion appeared less important to males than females. Mountain steppe habitats were used intensively in summer for denning and for foraging. As burrow density in mountain steppe was very high, the resource selection pattern suggested that dens were chosen in the most commonly used habitat to facilitate good access to foraging sites. However, the repeated use of individual dens indicated selection at a finer scale than tested here. Mountain steppe dens were traded for dens located in ravines in the winter, which was not highly selected for foraging during winter. Ravine dens may have functioned as an adaptive risk aversion strategy. As males foraged in steppe significantly more often in winter than summer (Chapter 4), ravines provided the most protective cover available within steppe and most probably influenced the decision of males to den there. While the locations of winter den sites had very good access to prey, the interpretative value of the data is unclear because males were actively seeking mates during winter, so siting dens for better travel access to mates was possibly the most important consideration.

Females were expected to select the safest den sites during the maternal period because of their large investment in reproduction. This prediction was born out, as females selected dens within rocky hillslope and ravines and with higher proportions of these habitats in the surroundings. The strength of selection for these habitats was greater for denning than for foraging. The selected habitats

provide the best hiding cover (Chapter 4), indicating that predation risk was an important factor in selecting maternal dens. While others have noted higher food availability in the vicinity of maternal dens (Pruss 1999; Szor et al. 2008), this did not appear to be true for Pallas's cats, as den sites were dominated by rocky hillslopes, which are relatively food-poor and Pallas's cats only eat mountain voles, the only small rodent living in rocky hillslopes, occasionally. Thus there is little relationship between den location and prey accessibility during the maternal period.

Females relaxed their selection of dens within safe habitat when not raising young, reflecting a similar change in their use of foraging habitats. The change could be associated with increasing access to foraging areas with higher prey density, although den selection still indicated substantially greater selection for safer habitats for denning than for foraging. The large change in denning behaviour between summer and winter also indicated compromises in safety in order to increase access to prey. In summer den habitat was the most important predictor of use, whereas in winter den habitat was not a predictor and the habitats in the den's surroundings were more important. The change suggested that females were prepared to use dens in any habitat, increasing their flexibility in foraging habitat use. Overall there was a substantial increase in the proportion of mountain steppe surrounding the den in winter; as mountain steppe is good pika habitat, the most frequently eaten prey species (Chapter 3), the change also indicated increased access to prey.

5.4.2. Is den selection dependent on season?

There were extreme changes in temperature between seasons (Chapter 1) and dens provided a means for Pallas's cats to thermoregulate, as being underground in marmot dens has a stabilising effect on temperature (Davenport 1992), while rock dens were cooler and more aerated. Dens thus provided warmer air temperatures in the cold winters and cool refuges in summer. Females took advantage of the thermal properties of dens; they stopped using rocky dens in winter, using marmot burrows instead. Winter dens also had significantly smaller entrance diameters, so restricting air circulation and increasing heat retention

(Kamnitzer 2008). The existence of air pockets within dens, which trap body heat, may also have been an important factor (e.g. Buskirk 1984).

There were large differences between summer and winter prey biomass. The differences were expected to be reflected in den selection because siting dens close to suitable foraging areas may provide energetic savings in terms of reduced daily travel and reduce exposure to predation (Buskirk 1989). Habitats surrounding winter dens had better foraging opportunities than dens selected in the summer. Though dens were not in the habitats with the best prey availability in either season, denning patterns suggest that safety influences denning and foraging behaviour and travel costs are taken into account when choosing dens sites.

5.5. Conclusions

Although the structure of dens is a likely attractant (Fernandez & Palomares 2001; Kamnitzer 2008), my analyses revealed that numerous environmental features surrounding the den are strongly related to den selection. While den selection was a reflection of Pallas's cats foraging habitats, the strength of selection patterns for dens were much stronger. Den sites were used on a daily basis by Pallas's cats and were involved in all aspects of the species life history, serving several important functions. However, selection patterns indicated that the overriding reason for den use was safety from sympatric predators. Thus most activities that did not require cats to be on the surface were done in the cover of the den. The keystone nature of the den resource indicates that the availability of suitable dens is likely to affect individual fitness and ultimately population persistence.

Chapter 6

A review of the conservation biology of Pallas's cat

Summary

- We currently have little understanding of how Pallas's cat may respond to the fragmentation of its habitat, yet the steppe ecosystem is coming under increasing pressure from development.
- Using available observations and data from my study in Mongolia, I produce a preliminary vulnerability profile of the Pallas's cat.
- While Pallas's cat has a relatively wide distribution and there are several intact undisturbed populations, its ecology indicates that it may be susceptible to future disturbances.
- Several ecological traits of Pallas's cat have been associated with increased vulnerability, including low population density, unusually large home range requirements and habitat and feeding specialisation.
- Pallas's cat is likely to require large intact areas to ensure its conservation, as its ecology indicates it will be particularly vulnerable to habitat fragmentation.

6.1. Forward

Trends in population and species extinctions have shown an accelerating decay of contemporary biodiversity that is projected to become worse in the coming decades (Ceballos *et al.* 2005; Pimm & Raven 2000). Efforts to stop the progress of extinction have stimulated the development of ecological theories of extinction risk and vulnerability, thus providing a framework to make predictions of the sensitivity of species' to environmental impacts (Purvis *et al.* 2000; Isaac & Cowlishaw 2004; Kotiaho *et al.* 2005; Cardillo *et al.* 2008). Effective conservation is only possible with an understanding of the limits and capabilities of species', therefore predicting vulnerability is an important step in the management and

prioritisation of species conservation (Baillie *et al.* 2004). In this Chapter I collate available data to produce a preliminary vulnerability profile of the Pallas's cat.

Dramatic changes in the Asian steppe ecosystem seem inevitable. An increasing livestock population is causing overgrazing, large scale mining of minerals is beginning, traditional nomadic lifestyles are being abandoned and climate change threatens to cause desertification (Bohannon 2008; Bulag 2009). Change is inevitable, but is also a universal feature of ecological communities (Groom *et al.* 2005); slowing the rate of change, increasing the sustainability of developments, and encouraging patterns of landscape utilisation that foster the coexistence of people and wildlife is the key challenge for conservationists.

Prior to my study information on Pallas's cat ecology and conservation was limited to mostly anecdotal accounts and observations (e.g. Heptner & Sludski 1992). Data describing their ecological relationships are however essential for an effective conservation strategy. To address this shortfall, I summarise what is known about Pallas's cats' ecology and use ecological theories of extinction and vulnerability to understand Pallas's cats' current vulnerability. I make the assumption that what we currently know about Pallas's cat is accurate, although interpretations may be inconclusive in the sense of lacking replication in other geographical locations.

6.2. The ecology and vulnerability of Pallas's cat

6.2.1. Foraging habitat utilisation

Habitat loss and fragmentation are the most pervasive threats for terrestrial species (Groombridge 1992; Ballie *et al.* 2004; Groom *et al.* 2006). Loss and fragmentation of habitat reduce population sizes resulting in increased probability of extinction by demographic and/or environmental stochasticity (Burkey 1995). Assessing the viability of a population therefore requires an understanding of the resources used, to determine how those resources affect long-term population persistence (Aldridge & Boyce 2008).

Pallas's cats use only a small fraction of habitats available to them, suggesting habitat specialisation. As the risk of predation is high from aerial and terrestrial carnivores, both of which are faster moving than Pallas's cats, their best line of defence is hiding out of sight and reach, and relying on camouflage. Rocky areas and ravines provide good disruptive cover and background matching properties and the high selection of these habitats probably helps Pallas's cat reduce its predation risk (Chapter 4). However, prey species resident in the rocky habitats were used only according to availability, whereas pikas, which did not use the rocky habitats, were highly selected (Chapter 3). Thus foraging for food mainly takes place on the edge of rocky habitats and within ravines where pikas are available. The selection patterns demonstrate the importance of habitats that are in or adjacent to pika habitat and have good cover from predation, as Pallas's cats were rarely found far from adequate cover.

Previous observations of Pallas's cats have also noted a strong association with upland steppes and rocky outcrops, suggesting that rocky upland areas are an optimal habitat for Pallas's cats throughout their range (Heptner & Sludski 1992). While caution should always be applied when extrapolating results to other areas, where larger terrestrial and aerial predators are sympatric, adequate cover is likely to be essential for population persistence. In open steppe habitats, this is most commonly provided by rocky outcrops and ravines, but shrub steppe may also provide this mix of cover and prey in less mountainous topography (e.g. Murdoch *et al.* 2006).

The habitat specialisation shown by Pallas's cat is cause for concern. For all species, there is a lower limit to the size of a patch that can act as breeding habitat. Farig (1997) demonstrated a threshold where 20% of the landscape must remain intact, as fragmentation beyond this seriously affected species' survival probability. As Pallas's cats are habitat specialists, suitable habitat in my study area was already reduced to 20-30% of the landscape before alterations by human activities. If habitat specialisation is always the case for Pallas's cat, then they are likely to be particularly vulnerable to habitat fragmentation.

6.2.2. Denning habitat utilisation

Denning habitat was selected to a greater degree than foraging habitats, and maternal den sites were selected more strongly than resting dens (Chapter 5). Maternal and summer resting dens were almost entirely located within rocky habitats, most likely to provide good anti-predator cover for kittens and for the cool and airy properties of rock dens in the summer. In winter, rock dens were not used; instead underground marmot burrows were preferred, most likely because they had good insulation and lower air circulation (Kamnitzer 2008). Denning preferences also suggested the existence of superior and inferior quality denning habitats and a fitness component to den utilisation, particularly in terms of reproductive fitness. In non-maternal individuals, the choice of den is most likely a trade-off between the vulnerability to predation when exiting the den, the thermal properties of the den and access to other required resources.

Although rock crevices were important, marmot burrows were the most commonly used denning resource. Considering they were used in all aspects of Pallas's cats' life including resting, giving birth and raising young, feeding, mating, predator avoidance and thermoregulation, marmot burrows are a critical habitat resource for Pallas's cats. While there is currently good availability of burrows within Pallas's cats' geographic range because of their sympatry with marmots (Figure 6.1 and 6.2), the loss of marmot burrows is now a concern because there has been a 70% decline in marmots in Mongolia in the last decade (Zahler *et al.* 2004). The loss of marmots could have dramatic effects on the landscape, but particularly on Pallas's cats as it seems unlikely that the population can persist without marmot burrows or suitable analogues.

6.2.3. Diet and feeding plasticity

In addition to habitat specialisation, evidence suggested Pallas's cat is a feeding specialist. Pikas constituted 53.8% of Pallas's cats' ingested biomass and were used disproportionate to availability indicating selection (Chapter 3). Pikas also appear to be to be the preferred food item in other parts of their range, for example pikas were present in 89% of scat samples collected in the Trans-Baikal (Heptner & Sludski 1992). Considering that only part of Pallas's cats' habitat preferences in my study area overlapped habitats used by pikas, prey selection for pikas was

very strong. While almost all other available food items were eaten, demonstrating an ability to generalise, the larger size of pika made them energetically very important. In situations where pika are not available as prey, then 3-5 times more captures would be required per day for Pallas's cats to satisfy their energy needs. So in the absence of pikas, the increase in costs per unit energy gain could result in a significant loss of fitness. It is likely that where Pallas's cats occur in areas without pikas, they do so at a much lower density (e.g. Figure 6.1 and 6.3).

The apparent dependency of Pallas's cats on pika may be problematic because of attempts to control or eliminate pikas in China and parts of Mongolia since 1958 (Smith *et al.* 1990, Smith & Foggin 1999; Clark *et al.* 2006; Smith & Xie 2008). Pika control programmes could have serious repercussions for Pallas's cats in terms of loss of food and secondary poisoning from rodenticides. While rodenticide campaigns have not been carried out in Mongolia since 2003, locals continue to use poisons at a small scale (A. Winters, pers. comm.). Poisoning campaigns in China are ongoing and have diversified to include pika contraceptives (Xin 2008; Watts 2009). In some cases these control measures have reduced pika populations to less than 5% of their pre-controlled densities, and may result in ecosystem-level disruptions that affect the whole biological community (Smith & Foggin 1999, 2000; Lai & Smith 2003). In particular, pika population reductions may result in an energy deficit, loss in fitness and a reduction in Pallas's cat population density, so pushing the population to local extinction. However, unless pika control is concurrent with other disturbances or the eradication of all prey, which is not improbable, Pallas's cat populations are likely to dip rather than crash. It is probable that Pallas's cats are already naturally exposed to large fluctuations in prey density and have a capacity to recover under suitable conditions.

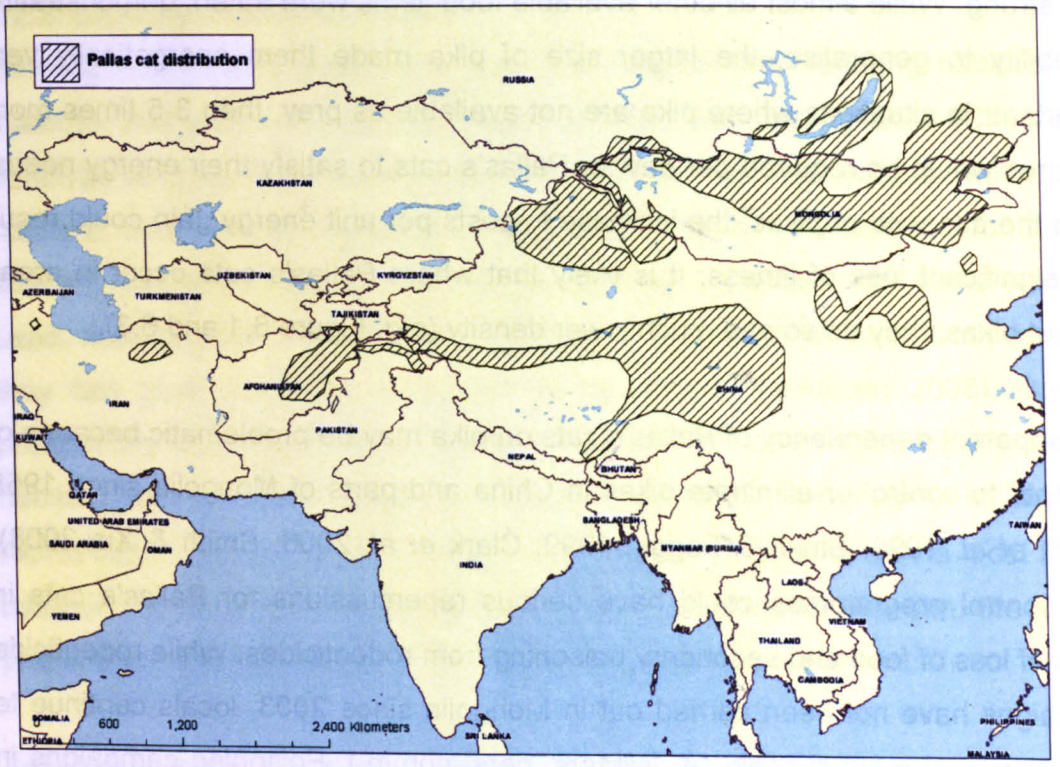

Figure 6.1: The current geographical distribution of Pallas's cat (Ross *et al.* 2008).

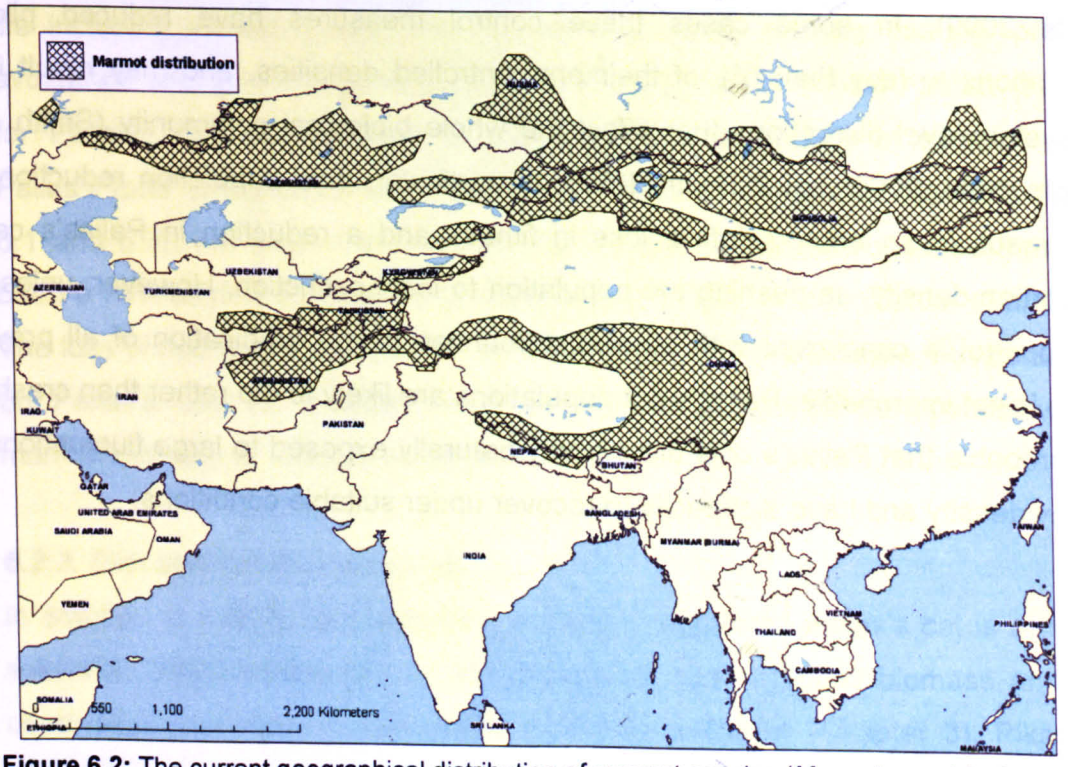

Figure 6.2: The current geographical distribution of marmot species (*Marmota* spp.) in Asia.

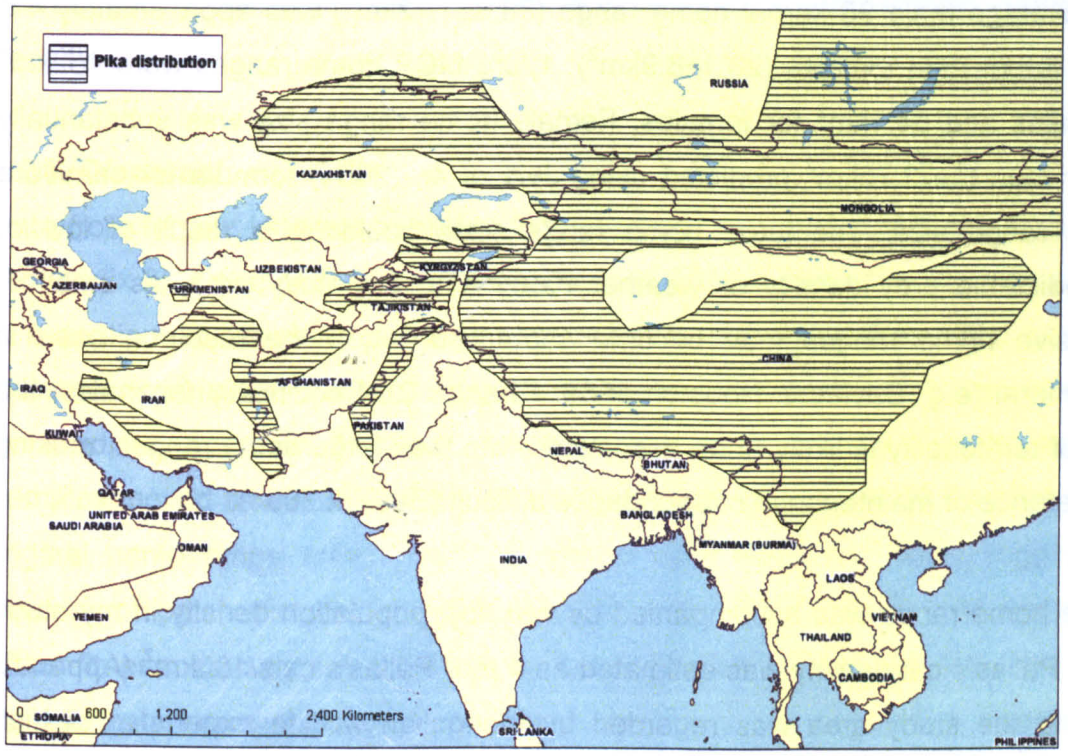

Figure 6.3: The current geographical distribution of pika species (*Ochotona* spp.) in Asia.

6.2.4. Social organisation, home range and density

As for many other cats, Pallas's cats are solitary. Males do not help raise kittens and, as a rule, they meet females only during the mating season. Male home ranges encompass one or more female territories in the typical polygynic system of solitary felids (Clutton-Brock 1989; Sandell 1989). However, unlike other felids, there was no indication that males monopolised individual females, as males had highly overlapping ranges (Seidensticker *et al.* 1973; Bailey 1974; Poole 2003). Several captured males had fighting injuries around the breeding period, indicating aggressive encounters and suggesting opportunistic rather than territorial control of mating (Chapter 2). In captivity, Pallas's cats spray and cheek-rub (Mellen 1993). Both behaviours provide temporal information for conspecifics and may serve to reduce the probability of agonistic encounters (Hornocker 1969; Schaller 1972; DeBoer 1977). In contrast female home range overlap was very rare, but appeared to be related to the low density of cats and the spacing of their preferred habitats, rather than territoriality.

The average male 95 kernel home range (98.8±17.2km^2) was approximately 4-5 times larger than females (23.1±8.9km^2); 100% MCP home ranges were 152km^2 for males and 64.1km^2 for females. Female home range size was substantially larger than the 2.75km^2 predicted using Jetz *et al.* (2004) formula for carnivore home range size. The large home range sizes could be a result of low or unpredictable prey density or weather patterns in the study area, as small or exclusive home ranges may become impractical when the resource base is ephemeral (e.g. Davies & Houston 1984; Chapter 2). Specifically for males, the lack of territoriality is likely to be associated with their large home ranges, making the defence or maintenance of boundaries difficult (Buskirk 2004).

Large home range was accompanied by very low population density in my study area. Pallas's cat density was estimated as 4 to 8 Pallas's cats/100km^2 (Appendix 2), and the study area was regarded by Mongolian wildlife experts as a high density area for the species (B. Munkhtsog, pers. comm.). The low density observed may be partially explained by Pallas's cats' specialised habitat niche constraining the population size through a restriction of available niche space. Low prey density is also a known determinant of carnivore density (Carbone & Gittleman 2002) and though prey density in the area appeared adequate, the presence of a number of other carnivore species, some of a similar size, means that interspecific competition may have had a limiting effect on Pallas's cat prey availability and therefore density.

Whatever the reasons for the large home ranges and low densities, both attributes influence extinction risk and require special conservation consideration (Woodroffe & Ginsberg 1998; Purvis *et al.* 2000). A large home range mediates interactions with human disturbances and increases edge effects (Harcourt 1998; Woodroffe & Ginsberg 1998). Since humans activities were responsible for 56% of Pallas's cat mortality, their large home range size is likely to be associated with more human interactions, additional mortalities and increased extinction vulnerability. Also, species that occur at low density should be more extinction-prone than those that occur at high density because, when isolated in fragments, their populations become smaller than those of co-occurring species with higher densities (Diamond *et al.* 1987; Robinson & Quinn 1988; Henle *et al.* 2004). Large areas will therefore

be required to maintain a viable population of Pallas's cats at their current low density.

6.2.5. Dispersal

Data from female kittens suggested that dispersal occurred at 4-5 months of age (Appendix 3). None of the kittens inherited part of their maternal range, or settled in a contiguous area. Instead, new ranges were established 5 to 12km from the maternal area (mean 8.8km). Large dispersal-like movements were also recorded for 9 adults (Appendix 3) which had previously been resident in home ranges. Females moved an average of 21.3km and males an average of 40.7km from their original home range area. The high rate of adult dispersal (50%) suggests a process of patch disturbance, where patches become unviable and negatively affect fitness, causing the inhabitant to leave (Hanski 1983). The low density of Pallas's cats also suggested many vacant patches in the population. Populations that experience high rates of patch extinction have been predicted to have higher dispersal rates than populations with low rates of patch extinction (Fahrig 1990; Fahrig & Merriam 1994).

The large distances moved and the travel across open habitat and rivers suggests that Pallas's cats have good dispersal abilities. Dispersal is generally viewed as having a positive effect on population survival through connection of metapopulations, reinforcement of small populations and recolonisation of areas where local extinctions have occurred (Hanski 1994). Thus dispersal ability may provide a population with resilience against localised disturbances (Wegner & Merriam 1990; Merriam & Wegner 1992; Villard *et al.* 1992). However, a high dispersal rate is also associated with greater requirements for intact habitat because the probability of colonisation depends not only on a species' dispersal behaviour, but the landscape the species is moving through, impediments to movement and its mortality within the landscape matrix (Farig 2001). As Pallas's cats had a very high adult emigration rate, and mortality rate of dispersers is believed to be high, population persistence in fragmented habitat is unlikely in the absence of immigration from larger populations (Matthysen 1999; Farig 2001). This susceptibility to habitat fragmentation requires that relatively larger areas of

intact habitat are needed for persistence and ways of limiting the mortality of dispersing cats is important for population management.

6.2.6. Reproduction and survival rate

Reproduction in Pallas's cats is highly seasonal and photoperiod-dependent (Brown *et al.* 2002); mating occurred between December and March and litters were born between the end of March and May. Males mated with 1 to 4 females, showing typical polygamy. Two males were also seen to pursue the same female in the same mating season, indicating the possibility of female promiscuity. Successful males shadow the female for 3-4 days (n=4), most likely guarding her oestrus (Clutton-Brock 1989), while the act of mating itself appears to take place inside dens (n=2), in both cases disused marmot burrows.

At approximately 3-4 months, kittens started to accompany their mother foraging. At 4-5 months they dispersed to establish a home range of their own before breeding in their first year. Three females in the study area successfully bred at the age of 9-10 months and raised litters; one 9-10 month old male was also believed to have sired a litter. Litter size in captivity averages 3.57±0.53, but ranges up to six or eight (Heptner & Sludskii 1992; Mellen 1993). Kitten survival in my study area was estimated by counting surviving kittens of 14 known litters at the end of July, just before dispersal. An average of 1.14±0.29 kittens survived (range 0-3), yielding a 31.9% kitten survival rate based on the average litter size in captivity. This is higher than has been recorded for feral cats (25%) and slightly lower than the norm for Canadian lynx, which has a 90% kitten survival rate during high snowshoe hare biomass, dropping to 25% during low hare biomass (Mowat *et al.* 1996; Nutter *et al.* 2004).

Kaplan-Meier log-rank analysis showed that adult male and female survival was not significantly different (χ^2=0.32, df=1, p=0.57), so sexes were grouped to estimate annual survival. On average Pallas's cats survived 27.1±2.1 months. Survival probability from dispersal at 4-5 months old until 12 months was 0.90±0.06; animals entering their second year had a 0.70±0.10 probability of surviving until 24 months, and animals entering their third year had a 0.50±0.09

probability of surviving until 36 months (Figure 6.4). Pallas's cats were killed by birds of prey (6), domestic dogs (6), local hunters (3), red foxes (1) and unknown causes (1). Mortality was biased towards winter, with 82.4% (n=17) of mortalities occurring between October and April. The winter coincided with poor vegetative cover, lower prey biomass and sub-zero temperatures. In addition female activity increased from February to April, most likely because of their declining reserves and the increase in prey activity towards the end of the winter. Males were highly active over the winter breeding season and males and females were significantly more diurnal (p<0.05) in winter than in summer (Appendix 1). The change in activity was accompanied by more use of open habitats during the winter; both changes in behaviour would result in cats being more vulnerable to mortality.

Since recruitment and survival are dependent on environmental conditions (Mowat *et al.* 1996), these data only represent a snapshot in time; I do not know if they are typical. At the measured rate of mortality, an average female surviving 27.1 months would only rear 2.28 kittens to dispersal age. Assuming dispersers survived and all females bred, this recruitment rate would lead to population stasis, since the breeding male and female would be replaced before death. In my study area better adult or kitten survival would be required to promote population growth; likewise higher mortality would lead to population extinction.

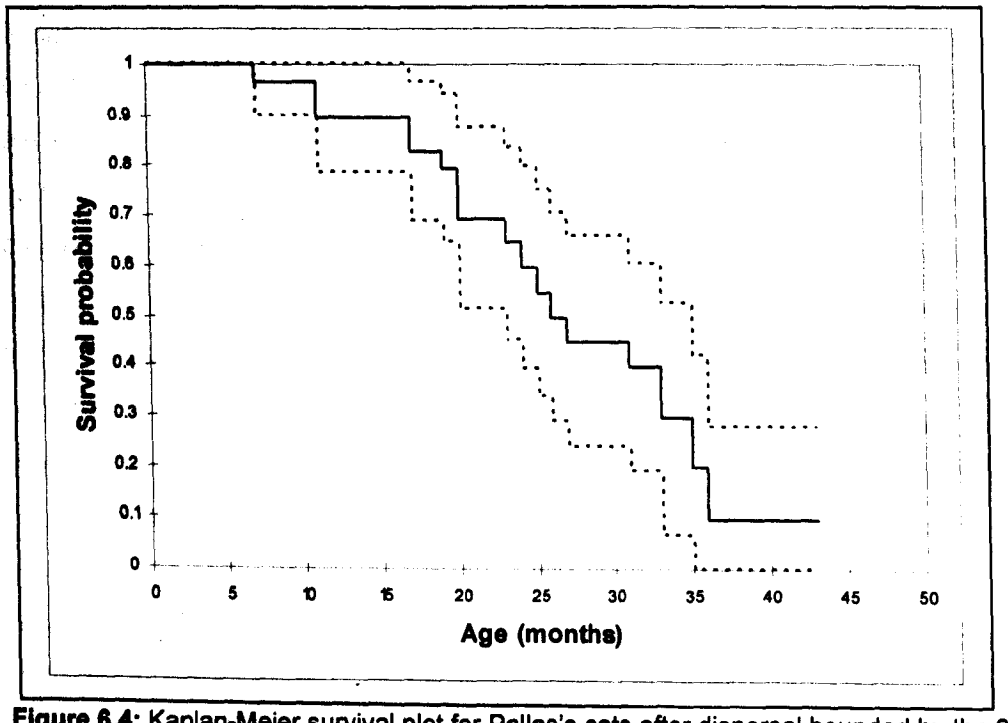

Figure 6.4: Kaplan-Meier survival plot for Pallas's cats after dispersal bounded by the 95% confidence intervals.

6.2.7. The limiting effects of sympatric carnivores on Pallas's cats

Interference competition between carnivores is increasingly recognised as an important factor structuring communities. Carnivores with inferior competitive abilities may be limited in their abundance and distribution due to direct killing and through avoidance of larger competitors (Laurenson 1995; Lindström *et al.* 1995; Palomeres & Caro 1999). Thus carnivore communities are structured in a hierarchical manner, with smaller competitors most often being less competitive than larger ones (Case & Gilpin 1974; Jones 1997; Donadio & Buskirk 2006). Competition can also be affected by habitat, as competition intensifies in open habitats, such as the steppe (Creel *et al.* 2001; Donadio & Buskirk 2006).

My data suggest that Pallas's cats were an inferior competitor to larger sympatric carnivores. Numerous deaths due to predation and observations of antagonistic encounters with sympatric carnivores, where Pallas's cats were the victim, provided evidence of competitive inferiority. Interference competition was probably accompanied by exploitation or feeding competition, as dietary overlap between the carnivores was extensive with all species preying upon the small mammal

guild (my unpublished data). Feeding competition can also be a factor precipitating interspecific killing (Polis *et al.* 1989; Palomares & Caro 1999; Donadio & Buskirk 2006). Predation risk was hypothesised to be the main factor influencing Pallas's cat habitat choices. This constrained Pallas's cats' use of habitat to only 20-30% of the study area, where there was suitable cover from predators. Competition therefore appears to have a limiting effect on Pallas's cat population density by reducing habitat availability. As well as direct top-down control of Pallas's cats, further limitations are probably imposed by competition for limited food resources, particularly during the winter.

Habitat disturbance tends to attract habitat generalists, such as the red fox (Baker & Harris 2007). Red fox density is therefore expected to increase if human populations and fragmentation in the steppe ecosystem escalates. The intolerance of nomadic herders to gray wolves may also see the local demise of this species if human population rises, this may result in meso-predator release (Crooks & Soulé 1999). Again the red fox is the likely winner under such conditions. The structure and organisation of the carnivore guild is therefore likely to see substantial changes in the future and these changes will have effects on the persistence of Pallas's cats.

6.2.8. Direct human influences and impacts

Direct human impacts in the study area included killing by poaching using rifles, killing by snares, injury by jaw traps and predation by domesticated dogs kept by local nomads. Human-associated mortality accounted for 56% of all mortalities recorded during the study, and so represents a significant limitation on population persistence. Anthropogenic mortality is also likely to be mainly additive to natural mortality, rather than compensatory, since mortality is unlikely to depend on the fitness of the individual. As Pallas's cats occur at low densities, additional mortality will have a relatively higher impact on the population and their vulnerability.

Although hunting of Pallas's cats has been regulated under Cites Appendix II since 1988, illegal trade continues and is evident in local Mongolian markets where Pallas's cat furs are freely available; Pallas's cats' body parts are also valued as traditional medicines (B. Munkhtsog, pers. comm.). Fortunately its fur is not highly

sought after and has a relatively low market value. Nevertheless, hunting in the study area accounted for 18% of mortalities and one additional injury. Pallas's cats were not a target of hunters but appeared to be shot or caught opportunistically while hunting for marmot, wolves or other species. However, hunting mortality is likely to be higher elsewhere, as my study may have discouraged hunting of Pallas's cats.

Predation by domestic dogs was a greater problem, causing 35.2% of all mortalities. Nomads have historically kept dogs and each nomadic family in the study area had 2-3 dogs to look after livestock, guard the camp and help while hunting. Domestic dog numbers varied throughout the year due to the nomadic movements of herders, reaching a high of 18 to 28 dogs/100km^2 during the winter and falling to 4-8 dogs/100km^2 in the spring when nomads moved out of the study area. All dog-caused mortalities occurred when dog density was high. People and dogs have a very loose relationship. Dogs are given water but fed infrequently and generally hunt to supplement their diet. Dogs also roam when seeking mates and are sometimes left with livestock or accompany herders. While away from the camp, dogs are more likely to come into contact with Pallas's cats; the loose relationship with the camp therefore contributes to predation levels.

While people around the world are giving up agrarianism for the city life, Mongolians are streaming in the opposite direction. The steppe ecosystem currently supports 35 million head of livestock, higher than ever before and more than 10 times the human population. As a result the sustainability of the grasslands have been impacted by overgrazing, which has been aggravated by a loss of traditional knowledge of rangeland management (Bohannon 2008). Considering the potential dangers associated with people, I expected Pallas's cats to avoid them; however Pallas's cats were found to be indifferent to nomad camps (Chapter 4). The likely link between mortality and being close to camps means that nomad camps are potential dangers to Pallas's cats. If there is a relationship between proximity to camps and mortality, there is likely to be a critical threshold density of human inhabitants beyond which Pallas's cats may not persist.

Perhaps of even greater concern however is the expanding human population and rapid economic development of Mongolia. The beginnings of an economic boom are expected to overwhelm Mongolia in the next decade, fuelled by the mining sector. Thirty-five per cent of the country's surface has already been licensed for mining exploration, and more than 80 minerals, oil and gas have been discovered (Knight 2007; Inman 2009). The mining boom is expected to increase the country's £3 billion gross domestic product by 25% in 2010 and then keep growing, year on year, at the same rate. Ultimately, mining will have serious economic, cultural and environmental impacts. To preserve ecosystem integrity while maintaining economic benefit, it is important that alternate options and environmental mitigation is evaluated so that the environmental costs of development are fully understood.

6.2.9. Recommendations for Pallas's cat conservation

Our best means of dealing with environmental impacts and reducing the current population decline is to use our knowledge of Pallas's cat ecology to guide ecosystem management. Following are recommendations and points of consideration to promote the conservation of Pallas's cat:

Resource management

1. As Pallas's cats are habitat specialists, larger areas will be required to account for the small proportion of the landscape utilised by them.
2. As marmot burrows are used for denning and provide important cover for Pallas's cats, future management needs to emphasise the preservation of marmots as a keystone species.
3. Evidence suggests that Pallas's cats are feeding specialist of pika. The conservation of pika populations should therefore be incorporated into any conservation plan for Pallas's cats, particularly where pika extermination programmes exist.
4. Habitat modification that favours generalist predators, such as habitat fragmentation (Oehler & Litvaitis 1996), is potentially detrimental to Pallas's cats due to the negative effects of interspecific competition.

Considerations concerning space use and dispersal

1. Pallas's cats are likely to need larger reserves for their conservation due to their large home ranges and low density. Priority should be given to measures that seek to maximise reserve size and mitigate persecution and reduce mortality on reserve borders and in buffer zones.
2. Pallas's cats have a high rate of adult dispersal, suggesting that a process of patch disturbance – emigration – colonisation forms part of their life cycle. Landscape connectivity is therefore important to permit colonisation of new patches, recolonisation of vacated patches and population persistence.
3. While Pallas's cats are capable dispersers, they are likely to experience high mortality rates from human and domestic dog interactions while dispersing. Further data are needed to understand what habitat features Pallas's cats could use to connect patches and how to reduce mortality in disturbed landscapes, as part of a habitat restoration approach.
4. Pallas's cat conservation will require an ecosystem management approach at the landscape scale; as populations are likely to become fragmented in the near future, habitat linkages between populations may be important to ensure the long-term viability of isolated populations.

Management of human impacts

1. Many Pallas's cats are killed by domestic dogs and the problem may require management intervention. Castration of non-breeding dogs can be effective at reducing roaming behaviour and reducing dog aggression (Neilson *et al.* 1997) and minimise dog-Pallas's cat encounters. More regular feeding of dogs would also lessen the tendency of dogs to hunt to supplement their diet.
2. Pallas's cats were found to be indifferent to occupied nomad camps. Nomad camps could therefore act as ecological traps, since the probability of human-induced mortality is expected to be higher near camps.
3. Indiscriminate and unregulated hunting is very common in Mongolia; while great improvements have been made in hunting regulation, the scarcity of many of the affected species means stricter regulation of hunting may be necessary.

6.3. Conclusion

It is difficult to know where and how many Pallas's cats there are because of its rarity and crypsis. This is an obstacle to designing a conservation plan. However, available evidence suggests that, from an ecological perspective, Pallas's cat's ecology predisposes it to extinction, although the assessment is constrained by the scarcity of scientific information. Certainly, within the Pallas's cats' range a substantial amount of their habitat is, or is likely to be, threatened in the near future, and there is no evidence that the species survives in association with anything but low density subsistence pastoralism. The research findings in this thesis have provided insights into important aspects of the conservation biology of the Pallas's cat, highlighting how its ecology relates to threats to its survival, within its typical steppe habitat. The work was strengthened by incorporating predictive modelling techniques within a robust ecological framework; improving our understanding of the underlying causes contributing to Pallas's cats' decline and helping to predict conservation issues for remaining populations.

The dominant influence on Pallas's cats' ecology was its susceptibility to predation. Anti-predator behaviour shaped all aspects of Pallas's cat's ecology including its habitat use, spatial behaviour, activity and where it rested, reproduced and fed. Predation pressure resulted in top-down limitation of the population, but also in specialisation for habitats with good cover and a dependency on marmot burrows and rock cavities as refuges. Feeding specialisation on pika was also shown, and was explained by Pallas's cats' optimal foraging strategy. While the increased dependence of Pallas's cat on specific habitat and food resources has an important ecological function, it also leads to less flexibility to changes in the resource base and thus increases their vulnerability to disturbances. Further extinction biasing traits were apparent in Pallas's cats' spatial ecology. Pallas's cat had the largest home ranges of any small cat studied to date and they lived at very low density. This was accompanied by a high rate of adult dispersal. Together these factors require that large areas of intact habitat are protected to facilitate the specialised needs of Pallas's cats'. The effect of biology on extinction risk is mediated by the environment a species inhabits. Pallas's cats were killed frequently by humans and domestic dogs suggesting that increasing human populations will limit Pallas's cats' directly and indirectly through habitat

fragmentation and disturbance. Overall, Pallas's cats' ecology paints a bleak picture for their future conservation. Considering the diverse changes that are currently sweeping through the steppe ecosystem, significant disturbance of Pallas's cats' habitat will continue to be an issue. The highest conservation priority for Pallas's cat is protection of their habitat.

On a more positive note much of the Pallas's cat population is currently located in isolated places, where large intact populations most likely still exist. A proactive ecosystem level conservation approach could provide a mechanism to protect these remaining populations. The management guidelines presented summarised some of the anticipated issues affecting Pallas's cat conservation; all issues are however dependent on the opinions and aspirations of the people who share Pallas's cats' habitat. Conservation efforts therefore need to proceed by providing local people with the biological, economic and social information they require to make informed decisions about their natural resources. Alternatives to unsustainable developments also need to be made clear. The extensive local expertise of biodiversity make sustainable options such as eco-tourism or sport hunting viable alternatives to development and require the Mongolian wilderness to remain intact. Considering the high value given to the wilderness by Mongolian people, sustainable alternatives may be deemed attractive.

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Appendix 1

The seasonal activity patterns of Pallas's cat

A.1.1. Introduction

Numerous factors are known to affect the activity patterns of mammalian carnivores, including diel temperature variation and behavioural thermoregulation (Chappell 1980; Schmidt-Nielsen 1983), competitive interactions with sympatric predators (Carothers & Jaksic 1984), limitations of the visual system (Walls 1963; Dunstone & Sinclair 1978), and risk of predation (Caro 2005). However carnivores are unique because their foods, unlike that of herbivores, have their own circadian cycles of availability (Zielinski *et al.* 1983; Zielinski 2000). Carnivores' activity times must therefore overlap the active period of their preferred prey, as well as avoid competition or predation from sympatric carnivores.

A.1.2. Methods

Activity monitoring was conducted using continuous 24 hour radio-telemetry surveys from the top of hills, where the signal of >3 Pallas's cats could be detected. Activity was evaluated by signal variation, where signals with erratic strength and pitch indicated active, moving animals (Nams 1989). Activity was assessed in this manner every 30 minutes for a minimum of 20 seconds (range 20-40 sec.) for each Pallas's cat within audible range. Hourly temperature, humidity and wind speed were concurrently recorded using a Kestrel 3000 Weather Monitor (Kestrel Meters, Sylvan Lake, MI, USA), which has an error of ±3% of the reading value.

Records were converted to percentage activity per 2 hour sample period for graphical representation. Percentage activity data were arcsine transformed and separated into time periods corresponding to diurnal, nocturnal and crepuscular (2 hours both sides of sunrise and sunset) activity; a one-way ANOVA was

conducted to assess differences between the activity periods, using cat identity as the sample unit. I used 2-sample t-tests to detect season differences in activity.

A.1.3. Results

Eight 24-hour activity surveys were conducted, covering the months June, July, September, October, November, December, January and February. This included a total of 33, 24 hour samples of females and 13 male samples, covering 13 individual females and 9 males (Figure A.1.1).

The sample covered temperature extremes from 28.5°C to -29 °C, a sand storm, rain and wind. Extreme weather conditions resulted in reduced activity, but did not prevent activity. There was no significant difference between male and female activity patterns. Pallas's cats were active at all times of the day and night but an ANOVA showed differences existed between activity periods ($F_{2,75}$=4.54, p=0.01). There was no overall difference between crepuscular and nocturnal activity periods (p=0.23), but activity was more crepuscular than diurnal (p=0.01). Seasonal differences in activity were detected. In summer ($F_{2,30}$=5.10, p=0.01), Pallas's cats were more nocturnal than diurnal (p=0.03) and more crepuscular than diurnal (p=0.02). In winter there were no significant differences between activity groups ($F_{2,45}$=2.81, p=0.07). While nocturnal activity was not different between seasons ($t_{1,25}$=0.04, p=0.97), cats were significantly more likely to be active during the day in winter than summer ($t_{1,22}$=2.97, p=0.007) and were more crepuscular during winter than in summer ($t_{1,28}$=2.16, p=0.04).

The number of hours Pallas's cats were active within a 24 hour period varied with season (Figure A.1.2). Females were least active during the summer whilst with kittens and most active during the period following kitten dispersal and in late winter. The periods of increased activity, September to November and February to March, coincided with times of energetic stress, indicated by low body mass, and also relatively high prey availability. Male Pallas's cats had one activity peak during the breeding period (January to March).

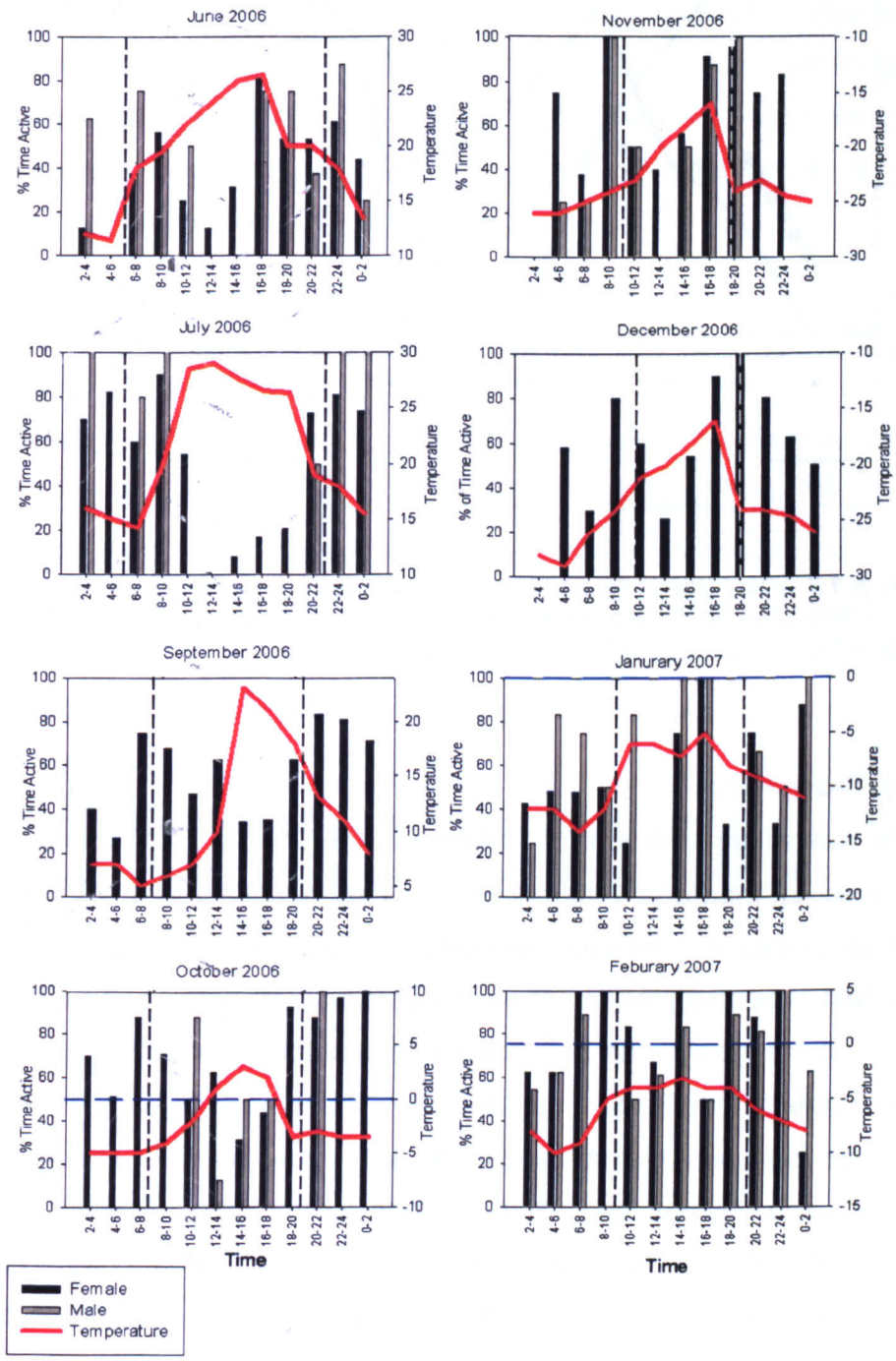

Figure A.1.1: 24 hour activity plots for female (black bars) and male (grey bars). Each activity period shows the average percentage time active within the two hour sample period. The vertical dotted lines indicate sunrise and sunset; the sold line shows temperature and the horizontal dashed lines show the 0˚C mark.

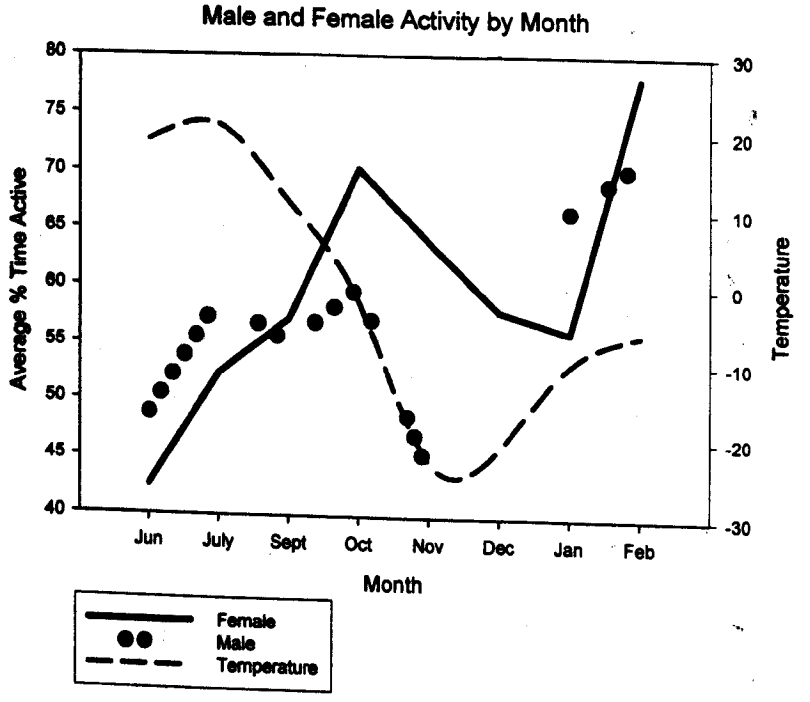

Figure A.1.2: Male (dotted line) and female (solid line) average percentage activity during 24 hour surveys. Also showing the average temperature experienced during each 24 hour activity survey (dashed line).

A.1.4. Discussion

There was a large amount of variation in the activity data collected. This can be explained by individual differences and may be partly due to resting behaviours such as grooming or head movement being wrongly recorded as activity. However the effect of resting movement on the data was expected to be minor. Pallas's cat activity in the study area coincided with a crepuscular activity peak. The activity peak suggests that Pallas's cat uses time to separate itself from predators, reduce predation risk and maximise overlap with prey activity. The majority of large raptors used thermal and wind updrafts for foraging (Jiménez & Jaksić 1989; Leshem & Yom-Tov 1996; Shamoun-Baranes *et al.* 2003), and had diurnal activity peaks, bounded by crepuscular activity lows on either side of the day and night. Pallas's cats' activity therefore served to minimise raptor encounters. The crepuscular activity peak would also minimise encounters and potential interference competition with red foxes, corsac foxes and gray wolves, as all are primarily nocturnal. Avoidance of these terrestrial carnivores may also reduce feeding competition (Palomeres & Caro 1999).

The majority of prey species were most active at daybreak and sunset, most likely because of lower aerial predator activity. Crepuscular activity was therefore an advantage for Pallas's cats' in terms of overlap with prey species. Pallas's cats crepuscular/diurnal foraging was confirmed by dietary analyses indicating the dominance of crepuscular/diurnal prey species, such as pika and mountain voles. Pallas's cat activity patterns would therefore promote avoidance of its main predators without sacrificing feeding opportunities.

The number of hours Pallas's cats were active in a 24 hour period changed over the year. The lowered activity shown by maternal females during the summer reflected time spent nursing and caring for young (Figure A1.2). The two activity peaks shown by females, following kitten dispersal and before giving birth in April were associated with very low body mass, and were before and after times of high energetic stress (winter and raising kittens). Female activity peaks also coincided with windows of relatively high prey biomass, suggesting that females increase activity when fitness is low and it is likely to have the most impact and when seasonal prey availability is high so maximising energy gains from increased foraging time. The heightened activity is likely to be an essential effort to balance and increase energy reserves before approaching periods of energy stress, and may be decisive in terms of influencing female survivorship during times of greater energy need.

Appendix 2

Pallas's cat density

A.2.1. Introduction

Rarity is a major determinant of a species' risk of extinction. In this sense rarity provides a useful basis for identifying those species in most need of conservation (Gaston 1994). In addition, descriptions of population density are an important monitoring tool and a means to compare the relative dynamics and habitat suitability of different populations.

A.2.2. Methods

I estimated Pallas's cat density in a 400km^2 core region of the study area that had the most collared Pallas's cats during the summer of 2007. The area was well covered by research activities, being traversed 2-3 times per week on motorcycle and giving confidence of the number of Pallas's cats in the area.

Density in the core area was estimated; where lower confidence intervals used data of the number of radio-collared Pallas's cats as the minimum number alive (μ), from direct observations of un-collared Pallas's cats or their tracks (τ), and an estimation of the minimum number of Pallas's cats believed to be resident, but not seen, based on the availability of suitable habitat. The upper confidence intervals were calculated using the number of radio-collared Pallas's cats as the minimum number alive (μ) and using knowledge of home range size and habitat selection patterns to estimate the maximum number alive (Slough & Mowat 1996). The formula for the density confidence intervals is illustrated below; the mean of the two confidence intervals was used as estimated density:

Lower CI = $\mu + \tau + \mu h$

Upper CI = $\mu + \varphi$

where: μ = Minimum number alive (8)
τ = all observed Pallas's cats over one year
μh = minimum suspected to be resident in suitable habitat
φ = maximum possible resident, using home range filling in suitable and marginal habitat

The estimation procedure was conducted within ArcGIS 9.2 and the number of male and female Pallas's cats was estimated separately to allow home range size to be considered more effectively.

A.2.3. Results

Pallas's cat density was estimated as 6.0 Pallas's cats/100km^2 with confidence intervals of 4 to 8 Pallas's cats/100 km^2. The lower confidence interval assumed that 8 uncollared Pallas's cats were resident within the 400 km^2 core area; whereas the upper confidence interval assumed that a further 24 uncollared Pallas's cats were resident in the core area.

In actual fact, only four further un-captured Pallas's cats were seen during the 2006 to 2007 period used for the density estimate. I am confident that this was in fact a large percentage, if not all, of the un-collared cats present for a number of reasons. The intensity of the research meant that I travelled on average 550 km cross country every week. Additionally, I spoke regularly to the 35 nomadic herders whom were resident in the area. The herders are outside year round tending their livestock and scanning the landscape with binoculars for wolves and their missing horses, so are an excellent source of information on wildlife, and they readily reported Pallas's cat sightings.

While the lower confidence limit (given 8 uncollared cats) seems reasonable, it is unlikely that the 24 uncollared Pallas's cats used in the upper estimate could have remained undetected, and the upper estimate is less realistic.

In comparison to other local carnivore density, measured using spotlight surveys and distance techniques (Buckland *et al.* 2001), Pallas's cats' density in the study

area was low. Corsac fox density was approximately 40-60/100km^2; red fox density was 15-25/100km^2 and gray wolf density was 3-20/100km^2

A.2.4. Discussion

Due to the very cryptic nature of Pallas's cats the density estimate was designed to be optimistic to account for the uncertainty of further unknown Pallas's cats being resident. It is common practice to use only radio-collared or live trapped animals as the lower confidence interval, rather than adding unknown animals into the calculation, as was done here (Slough & Mowat 1996).

Within the study area Pallas's cats existed at a low density of approximately 6 individuals/100km^2. Many reasons have been proposed to explain the low density nature of some species, however rarity is not believed to be an adaptive strategy, even though individual organisms may benefit from the rarity of the species as a whole (Gaston 1994). Undoubtedly, one reason for Pallas's cats' low density in my study area was the scarcity of their habitat. Pallas's cats used only 20-30% of the available habitats, thus their specialised niche restricted the potential population size through restriction of available niche space. Competition may also have been involved, as intra-guild predation was believed to be the main factor causing Pallas's cats' specialist habitat preferences.

It is important to assess whether rarity is a range-wide characteristic of Pallas's cats or merely a local phenomenon. Several studies of Pallas's cat have indicated that low density is likely to be range-wide: (1) a study in Ihk Nart in southern Mongolia spent 3-years trapping for Pallas's cats and succeeded in capturing only three (Murdoch *et al.* 2006). Interviews carried out in Ikh Nart by myself also indicted that the species was not well known and had never been seen by locals; (2) snow tracking surveys of the Pallas's cat have been conducted in several federal republics of Russia, claiming Pallas's cat densities of 0.1 Pallas's cats/100km^2 in Buryatia, 0.5 Pallas's cats/100km^2 in Altai and 1.2 Pallas's cats/100km^2 in Tyva (Barashkova *et al.* 2007). The estimates are for the whole region studied and therefore include unsuitable habitats in the calculation of density, which lowers overall density; (3) Pallas's cat is poorly known throughout

their range, it is rarely seen and there is little traditional lore regarding the species. These three points provide circumstantial evidence supporting the view that Pallas's cat is an intrinsically low density species.

Appendix 3

Natal and adult dispersal by the Pallas's cat

A.3.1. Introduction

Dispersal of an individual has consequences not only for individual fitness, but also for population dynamics, genetics, and distribution (Hanski & Gilpin 1997; Hanski 1999). Due to the close link with population dynamics, gaining insight into dispersal rates, success, causes and consequences is vital for population management and predicting responses to environmental changes (Bowler & Benton 2005). Dispersal is generally viewed as having a positive effect on population survival through connection of metapopulations, reinforcement of small populations and recolonisation of areas where local extinctions have occurred (Hanski 1994). Thus dispersal ability may provide a population with resilience against localised disturbances (Wegner & Merriam 1990; Merriam & Wegner 1992; Villard *et al.* 1992). In Appendix 3 I use opportunistic data measuring dispersal of radio-collared kittens and late dispersal by adults to understand the nature of and reasons for dispersal in Pallas's cats.

A.3.2. Methods

Pallas's cats were radio-collared as described in Chapter 2, and radio-collared Pallas's cats' movements were followed using telemetry.

A.3.3. Results

A.3.3.1. Natal dispersal

Three kittens were captured and radio-collared at the age of 4-5 months, while still in their natal home range. Dispersal distance was measured from the point of capture to a point of stabilisation. In all cases the capture site was believed to be

approximately in the centre of the natal home range. Kitten 1 and 2 were from the same cohort.

Table A.3.1: descriptions of natal dispersal, establishment of a home range and first year breeding activity for 3 female kittens.

Kitten 1	Gradually dispersed 9.5km SE starting on the 20th of August. She established her home range area by the end of September when 6.5 months old. She successfully bred in February 2007 at the age of 10 months.
Kitten 2	Gradually dispersed 12km SEE, taking a very convoluted route before establishing a home range area by December 2006 at 8 months old. She successfully bred in February 2007 at the age of 10 months.
Kitten 3	Gradually dispersed 5km SE before establishing a home range at the start of October at 6.5 to 7 months old. She successfully bred in February 2007 at the age of 10 months.

A.3.3.2. Late dispersal or emigration by adults

Late dispersal or emigration was recorded for 9 adults; 6 of these were followed long enough to describe the movements. A total of 50% of radio-collared Pallas's cats that were capable of emigration (survived >1.5 years old) did so, indicating the prevalence of this behaviour. In all cases the adult had an established home range area which had been maintained for ≥1 year. All dispersal events were precluded by a small increase in home range size before sudden dispersal. August to October was the favoured time of dispersal (7 of 9). This period is typified by calm weather, moderate temperatures and good prey availability.

Table A.3.2: descriptions of late dispersal for 3 female and 3 male Pallas's cats.

Female 1	Maintained a home range in a relatively small area of 20km^2 before moving 18km SW on the 20th of September. Her signal was then lost, indicating she went further.
Female 2	Maintained a home range in a small 10km^2 area before moving 21km south on August 1st (most likely immediately after kitten dispersal). Her signal was then lost indicating she went further.
Female 3	Maintained a home range the previous winter before moving 25km NE at the end of March; she stabilised her home range for a short time while with kittens, then maintained a very large home range of 200km^2 from June to November before her signal was lost at the end of November. She was either killed by hunters or went greater than 40km from the study area.
Male 1	Maintained a home range before moving 25km to the SW in October. His signal was then lost indicating further movement in the same direction.
Male 2	Maintained a home range before moving 45km NE in August crossing a 15m wide and 2m deep river in the process. He returned to his home range area two weeks later and then again crossed the river and moved 50 km to the NE where he remained until the end of the study.
Male 3	Maintained a home range before dispersing on the 1st of May. He moved 52km NE crossing a 12m wide 1.5m deep river and then commenced an exploratory loop over the summer with short periods of area fidelity. He re-crossed the river to the study area in October and settled in the study area after completing a 170km movement loop over a 2-month period. He bred successfully in the study area in a home range 7km from his previous winter range, remained for 6-months before again dispersing 50km in the same direction the following May. If measured as a home range, male 3 had a summer home range size of 1040km^2.

A.3.4. Discussion

The large distances moved and the fact that two of the adult males crossed 6km-wide tracts of unused habitat and swam across 12m-wide rivers suggests that Pallas's cats have good dispersal abilities. Dispersal is generally viewed as having a positive effect on population survival through connection of metapopulations (Hanski 1994). However in fragmented landscapes or landscapes where mortality risk is high outside of the species habitat, a high rate of adult dispersal may have a negative effect on the population by decreasing the average survival rate. Adult dispersal was extremely common in Pallas's cats (50%) and is high in comparison to other mammals (Farig 2001). Three hypotheses were proposed as possible reasons or mechanisms influencing the high rate of adult dispersal.

A.3.4.1. Hypothesis 1: Low prey abundance causes dispersal

Adult dispersal has been documented for Canadian lynx (O'Donoghue *et al.* 1995; Poole 1997) and bobcats (Bailey 1974); both cases of dispersal (or emigration) were during periods of low prey abundance caused by prey cyclicity, where a lack of food was suspected to cause dispersal. Poole (1997) described late dispersal as environmental dispersal because of its dependence on prey abundance. Dispersal of lynx peaked during the prey decline in south-central Yukon (Slough & Mowat 1996), indicating that lynx are able to detect the collapse of resources and react spatially. Lynx that didn't disperse in the Yukon population died (O'Donoghue *et al.* 1995).

Evidence suggested that low prey abundance was not a factor related to adult dispersal in Pallas's cats: (1) because adult dispersal occurred during 2006 and 2007, which were years with high prey abundance; (2) although evidence regarding prey availability in the pre- and post-dispersal ranges of cats was lacking, the distances travelled (18-52km) should not affect local environmental conditions such that food abundance changes. Moreover, Pallas's cat home ranges were large enough that richer food patches should have been available if sought.

A.3.4.2. Hypothesis 2: Intra-species competition causes dispersal

Intra-species competition is unlikely to be the reason for late dispersal because competitors would be the young of the year dispersing from their natal territory. Young Pallas's cats would be at a size disadvantage (2.5 - 3.0kg vs. 3.8 - 5.0kg) and the asymmetry of the interaction would most likely result in poorer competitive ability of incoming Pallas's cats.

A.3.4.3. Hypothesis 3: Inter-species competition causes dispersal

Late dispersal occurred at a time of year coinciding with peak annual density of red and corsac foxes due to the spilling out of the young of that year into the surrounding landscape. Red foxes are seeking territories during autumn and are capable of exerting interference competition on resident Pallas's cats. Raptors, such as steppe eagles, upland buzzards and eagle owls could also exert greater

localised predation pressure during late summer due to formation of groups of parents and offspring greatly increasing the local density of raptors.

Although one would assume that increases in predation pressure could be avoided by using another part of the home range, it is feasible that such predation pressure and the fear of death or injury forces Pallas's cats to disperse. The distance travelled may be necessary in order to find a suitable vacant territory.

Theories explaining the spatial consequences of interspecies competitive interactions between mammals are few because of the difficulties of studying multi-species interactions in mobile animals, more advances have been achieved in plants. Tilman (1994) modelled and described a system of competition and co-existence in plants. The model outlined a fundamental trade-off among competing species – the ability to hold a site (being a good competitor), verses the ability to get to a site (being a good coloniser). The system led to the superior competitor taking the place of the previous occupant, coexistence was facilitated through the ousted competitor's superior ability at dispersing and finding new un-occupied patches. Mammal species are known to be either good or poor dispersers, a trait that is thought to be related to the metapopulation dynamics of species (Fahrig & Merriam 1994).

Dispersal is a similarly risky endeavour for insects as for mammals and thus may provide a good model system in which to understand predation induced dispersal. Dispersal conditional on the presence of predators or an increase in the risk of predation in habitats has been shown repeatedly in insects (Weisser 2001). For example, spider mites leave plants in the presence of predatory mites (Bernstein 1984). Similarly, pea aphids are more likely to leave a host plant if a predatory ladybird is in the vicinity (Roitberg *et al.* 1979). Predatory aquatic stoneflies induce a variety of insect prey to disperse from the population by drifting (Sih & Wooster 1994). Similarly, there is an increased rate of flight polymorphisms (ability to fly; a dispersal polymorphism) in pea aphids under the influence of ladybird predation, than in its absence. In all cases, individuals leave to reduce their immediate mortality risks. Predation in insects is an evolutionary force that may result in

dispersal strategies, such as dispersal conditional on predator attack or an increase in the risk of predation (Weisser 2001).

Similar studies of larger mammals have not yet taken place, but the pressure of interspecific competition and predation has recently been reviewed (Palomeres & Caro 1999; Donadio & Bushkirk 2006). The reviews have highlighted the importance of interference competition to mortality and fitness of its victims. Indirect effects of the 'fear' of predation have been documented in red foxes, which used only the periphery of coyote home ranges and different habitats from coyotes where they occurred in sympatry (Sargeant *et al.* 1987; Theberge & Wedeles 1987). Similarly, avoidance of wolf home ranges by coyotes has been shown (Fuller & Keith 1981). Wild dogs and cheetah are known to avoid areas where lions are common (Mills & Gorman 1997; Durant 1998) and European genets and Egyptian mongooses avoid suitable habitats where densities of Iberian lynx are high (Palomares *et al.* 1996). Of course the above examples are cases of avoidance, of niche partitioning, a phenomenon long believed to be an integral part of species co-existence. However it is a short step to hypothesise that superior and feared competitors cause the displacement of their inferiors.